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THE EVOLUTION OF THE HUMAN BRAIN
1979

THE FOSSIL RECORD OF PRIMATE BRAIN EVOLUTION

LEONARD RADINSKY

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THE FOSSIL RECORD OF PRIMATE
BRAIN EVOLUTION

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†Published version: *The Brain in Hominid Evolution*, New York: Columbia University Press, 1971.

THE FOSSIL RECORD OF PRIMATE BRAIN EVOLUTION

INTRODUCTION

The fossil record of primate brain evolution consists primarily of endocranial casts, or endocasts, which are casts of the inside of the braincase. Endocasts of most mammals reproduce the external morphology of the brain, because in life the inner surface of the braincase conforms closely to the configuration of the brain. Fossil endocasts are the only evidence we have of the brains of extinct mammals, and they can provide information on brain size, shape, and patterns of cerebral convolutions. In relatively large brained mammals, such as the living great apes and humans, impressions of cerebral convolutions are blurred or absent, and endocasts provide information only on brain size and shape. However, in smaller brained primates, such as prosimians and most monkeys, endocasts can reproduce all of the cerebral convolutions, and also some details of cerebellar morphology. (Bauchot and Stephan, 1967; Radinsky, 1968, 1972).

Endocasts can be prepared in two ways. If the matrix filling a fossil braincase is relatively hard, the bones of one side of the braincase can be stripped away to expose the natural stone endocast. If the matrix is soft, the braincase can be cleaned out and an artificial endocast prepared with liquid latex (see Radinsky, 1968, for the latter technique).

The external brain morphology revealed by fossil endocasts can be interpreted by extrapolating from the work of neurophysiologists on modern brains. Cortical mapping studies have shown that major functional areas are localized, and in brains with convolutions, functional areas may be delimited by sulci (grooves). Thus, by extrapolating from cortical maps of living primates (fig. 1), one may infer the functional significance of differential enlargement or reduction of parts of the brain seen on fossil endocasts. Such functional inferences are hypotheses that

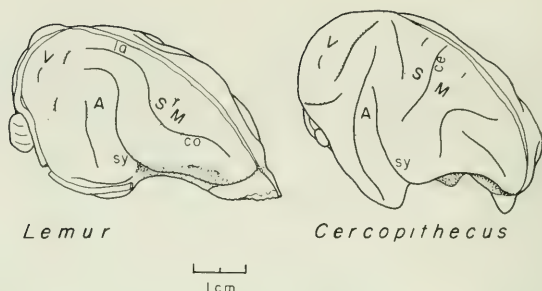
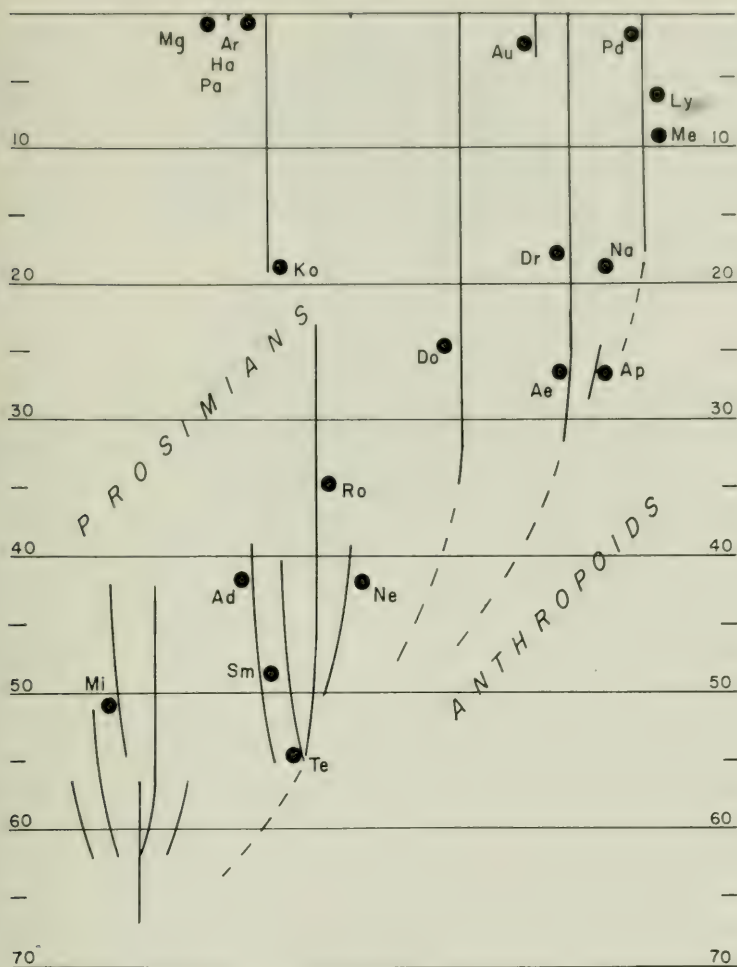


FIG. 1. Endocasts of a modern prosimian, *Lemur variegatus*, and a modern anthropoid, *Cercopithecus talapoin*, to show differences in cortical folding patterns and relationships of major sensory and motor cortical areas to sulci. Location of functional areas extrapolated from cortical mapping studies of a variety of modern primates. Abbreviations: A, auditory cortex; ce, central sulcus; co, coronal sulcus; la, lateral sulcus; M, primary motor cortex; S, primary somatic sensory cortex; sy, sylvian sulcus; V, primary visual cortex.

cannot be tested directly, but can be strengthened (or weakened) by correlations with other bits of evidence. For example, one would expect expanded visual cortex to be correlated with enlarged orbits, expanded auditory cortex with enlarged auditory bullae or modified auditory ossicles, and expanded facial somatic sensory (tactile) cortex with an enlarged infraorbital foramen (transmits nerves and blood supply to face).

Another source of information for interpreting fossil endocasts is comparative anatomical studies of the brains of living species. There are still only a few broad comparative studies of the neuroanatomy of living primates, and the most important of these for interpreting endocasts are the work of Bauchot, Stephan and colleagues (Stephan, Frahm and Bauchot, 1977, and references cited therein). They have provided a substantial amount of information on the gross anatomy and the relative sizes of major parts of the brain of a large number of primates and insectivorans, and those data provide a context against which various aspects of fossil endocasts can be compared.

Endocasts are known from only a small number of fossil primates (fig. 2). This is because primates are, with a few exceptions, relatively rare in the fossil record, and uncrushed



braincases, from which endocasts can be prepared, are even rarer. I have reviewed much of the fossil record of non-hominid primate endocasts (Radinsky, 1970, 1974, 1977), and fossil hominid endocasts have been discussed recently by Holloway (1975, 1976) and Kochetkova (1978). Some new evidence, plus the desire to reassess some of the old evidence, provided the impetus for this review.

EARLY PROSIMIAN ENDOCASTS

The oldest good evidence of early primate brains is an endocast of *Tetonius*, an omomyoid prosimian from the early Eocene (about 55 my) of Wyoming. The brain of *Tetonius* was advanced over the primitive condition (seen in most insectivorans) in having a more expanded neocortex (rhinal fissure not visible in dorsal view), with the expansion most apparent in occipital and temporal regions (fig. 3). The brain of *Tetonius* was primitive compared with those of modern prosimians in having a relatively small frontal lobe (here taken as the neocortex rostral to the sylvian fissure). The olfactory bulbs appear relatively small in *Tetonius* compared with the primitive condition, but that may reflect either expansion of the neocortex or reduction in size of olfactory bulbs, or both (see discussion below). Except for the faint impression of the sylvian fissure, the neocortex of *Tetonius* was unconvoluted. That lack of sulci should not be considered a primitive feature relative to later primates, since small modern primate brains show a similar condition.

Endocasts are known for two other early omomyoid prosimians: *Necrolemur*, from the late Eocene of Europe (about 40 to 45 my), and *Rooneyia*, from the early Oligocene (about 35 my) of Texas. The endocast of *Necrolemur* (fig. 4) was larger than that of *Tetonius* but otherwise apparently similar in proportions and preserved morphology. The *Rooneyia* endocast (fig. 4) suggests a brain more advanced than that of the older omomyoids in having a relatively larger frontal lobe and relatively smaller olfactory bulbs. However, the frontal lobes appear to have been

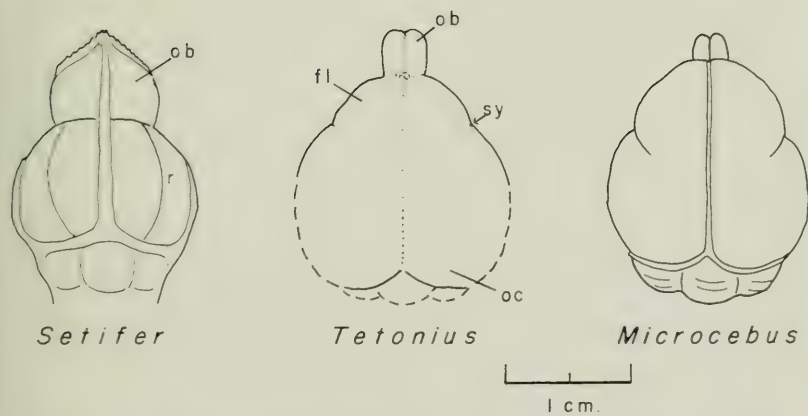


FIG. 3. Top, skull of *Tetonius homunculus*, showing natural endocranium. Scale on right is 1 cm. long. Bottom, restoration of *Tetonius* endocranium, compared with endocraniums of a modern insectivoran, *Setifer setosus*, and a modern prosimian, *Microcebus murinus*. Abbreviations: fl, frontal lobe; ob, olfactory bulb; oc, occipital lobe; r, rhinal fissure (=lateral boundary of neocortex); sy, sylvian sulcus. All three drawn to same scale (from Radinsky, 1975).

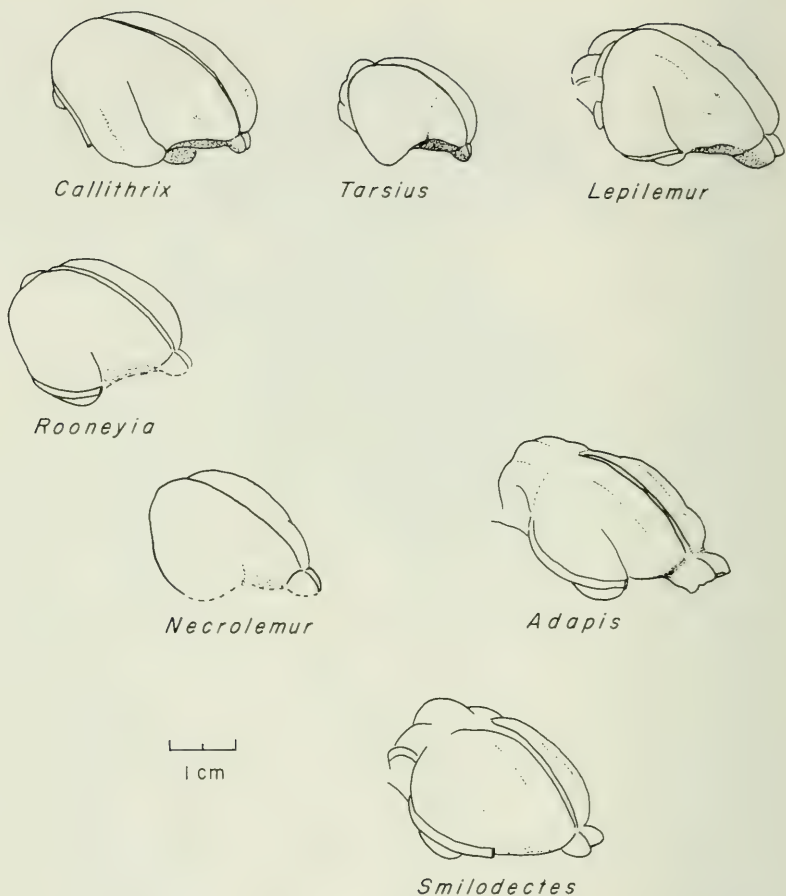


FIG. 4. Fossil prosimian endocasts compared with those of modern prosimians (*Tarsius* and *Lepilemur*) and a modern anthropoid (*Callithrix*). See text for discussion, and Radinsky (1970), for dorsal and lateral views of the fossil endocasts. All drawn to same scale.

relatively smaller in *Rooneyia* than in modern prosimians, and a modern prosimian brain the size of that of *Rooneyia* would have other sulci in addition the the sylvian fissure.

The other main branch of Eocene prosimians, the adapoids, is represented by endocasts of three genera: the closely related *Smilodectes* and *Notharctus*, from the middle Eocene (about 48

my) of Wyoming, and *Adapis*, from the late Eocene (about 40 to 45 my) of Europe. The brain of *Smilodectes* (fig. 4) lacked a sylvian fissure, and the cerebrum did not overlap the cerebellum. However, there was a longitudinally oriented neocortical sulcus that paralleled the dorsal midline, and, in one of the two known endocasts, a rostromedially oriented sulcus situated more laterally. The cerebrum of *Smilodectes* was relatively short, broad and shallow compared with that of the omomyoids, and the olfactory bulbs appear to have been relatively smaller than in *Tetonius* and *Necrolemur*. One partial endocast of *Notharctus* suggests a brain similar to that of *Smilodectes*.

The brain of *Adapis* (fig. 4) was similar to that of *Smilodectes* and *Notharctus* in being relatively broad across the temporal region, and in having a longitudinal sulcus near the dorsal midline and a dorsally exposed cerebellum. However, *Adapis* was advanced over the middle Eocene genera in having a well-developed sylvian fissure and a more expanded frontal lobe. The frontal lobe appears to have been relatively smaller in *Adapis* than in modern prosimians (compare with *Lepilemur* in fig. 4).

Accurate estimates of relative brain size in the early prosimians just discussed are not possible because we have as yet no good estimates of body weight for these genera. In my early studies of fossil prosimian endocasts (e.g., Radinsky, 1970), I estimated relative brain size using foramen magnum area as a substitute for body weight. However, partial correlation analysis shows that while foramen magnum area is a reasonable estimator of body weight in some groups of mammals, it is not a good estimator of body weight for relative brain size comparisons in prosimians (Radinsky, unpublished data). Fleagle (1978) inferred body size of fossil primates from lower molar lengths, based on Kay's (1975) analysis of this relationship in modern primates. However, as Kay noted, molar size-body weight relationships in modern primates vary significantly between the major dietary types. Thus consideration of dietary specialization is necessary for estimating body weight from tooth size in primates. Jerison (1973) and I (1977) have estimated relative brain size in fossil prosimians with body weights estimated very approximately from skull size. My

estimates, which are lower than those of Jerison, place *Tetonius*, *Smilodectes*, and *Adapis* within the insectivoran range, below the modern prosimian range, and *Necrolemur* and *Rooneyia* within the lower half of the modern prosimian range. In view of the uncertainties involved in the body weight estimates, I would not place much significance on those relative brain size estimates.

INFERENCES

The early prosimian endocasts described above indicate that by the beginning of the Eocene the neocortex had expanded beyond the primitive condition still seen today in most insectivorans. In the omomyoids, neocortical expansion is most apparent in occipital and temporal regions, which suggests expansion of visual and possibly also auditory cortical areas. The skulls of *Tetonius*, *Necrolemur*, and *Rooneyia* (see Szalay, 1976) have relatively large orbits and large, ossified auditory bullae, compared with the primitive condition seen in most insectivorans. Thus, the peripheral anatomy supports inferences from the endocasts of increased importance of vision and auditory abilities. Since those specializations appeared 55 million years ago, at the base of the great Eocene omomyoid radiation, it is possible that they were among the adaptations responsible for that radiation.

In the adapoids, the occipital pole had not expanded back to overlap the cerebellum, as in the omomyoids, and neocortical expansion is most evident in the temporal region. Extrapolating from cortical maps of modern mammals, this also suggests visual and possibly auditory specialization. The skulls of *Smilodectes*, *Notharctus*, and *Adapis* have inflated, ossified auditory bullae, supporting the inference of auditory specialization over the primitive condition, but the orbits do not appear to be relatively large. Relatively smaller orbits than in omomyoids may be a reflection of the larger size of the adapoids, since eyes scale with negative allometry (i.e., are relatively smaller in larger forms), and without better comparative series, it is not obvious if orbits are enlarged over the primitive condition in the adapoids.

The olfactory bulbs appear relatively small (compared to brain size) in the early prosimians, and in previous papers (Radinsky, 1970, 1975) I inferred from that condition reduction in importance of olfaction. However, relative size of olfactory bulbs can be deceptive, since expansion of neocortex with no reduction in size of olfactory bulbs can give the appearance of reduced olfactory bulbs (as noted by Martin, 1973, p. 327). The analysis of olfactory bulb size compared with body weight in modern insectivorans and primates (Stephan and Andy, 1969) reveals several species of modern prosimians with olfactory bulbs that appear small relative to the rest of the brain but which fall within the insectivoran range when compared with body weight. If the relative brain size estimate for *Tetonius* is correct, and it fell within the insectivoran (=primitive) range, then its small olfactory bulbs (relative to brain size) would indeed indicate reduction of olfactory bulb size from the insectivoran condition. However, until we have better body weight estimates for the early prosimians, we have no good basis for inferences on the relative importance of olfaction.

There appears to be an increase in relative frontal lobe size (here taken as the cortex rostral to the sylvian fissure relative to the rest of the brain), in *Rooneyia* compared with the earlier omomyoids, and in *Adapis* compared with *Smilodectes*. However, even in *Rooneyia* and *Adapis*, the frontal lobe appears smaller compared with the rest of the brain than is the condition in modern prosimians (excluding *Tarsius*). The frontal lobe (as here defined) contains the primary somatic sensory (tactile) and motor areas, as well as "association" cortex, and I see no way to infer significance of changes in its relative size.

The early prosimians discussed above evolved in the second adaptive radiation of primates. The earliest primates appeared around 70 million years ago, and underwent a first evolutionary radiation between about 65 to 55 million years ago (see fig. 2). An obvious question is whether the brain specializations noted for the Eocene prosimians (expanded neocortex, apparent expansion of visual and possibly also auditory areas, possible reduction in size of olfactory bulbs) also characterized their Paleocene prede-

cessors. Unfortunately, there is almost no direct evidence of the brain in the Paleocene primates (see discussion in Radinsky, 1977). The most significant information comes from the analysis by Kay and Cartmill (1977) of a partial skull of *Palaechthon*, a middle Paleocene (60 my) paromomyid primate. Relatively small orbits, a large olfactory fossa, and a large infraorbital foramen suggest the primitive insectivoran condition of emphasis on olfaction and tactile vibrissae (blood and nerve supply *via* the infraorbital foramen), and relative unimportance of vision in this 60-million-year-old primate. Thus it appears that the emphasis on vision that characterizes later primates was not involved in the origin of primates but rather evolved in connection with their second evolutionary radiation at the beginning of the Eocene.

LATER PROSIMIAN ENDOCASTS

The fossil record of later prosimian endocasts is poor, making it difficult to pinpoint when modern proportions and relative size of brain were attained. An endocast from the Miocene of East Africa, (probably 15 to 20 million years old), referred to the lorisoid *Komba*, is the only other Tertiary prosimian endocast known. It reveals that modern frontal lobe size and modern sulcal pattern were attained by that time (Radinsky, 1970). The only other fossil prosimian endocasts known are from several large to gigantic extinct Malagasy lemuroids from the latest Pleistocene or subrecent. While they shed no light on the evolution of modern prosimian brains, they are of interest for extending our knowledge of how allometry can affect gross brain morphology.

The long-faced giant lemuroids, like *Palaeopropithecus* and *Megaladapis*, show two unusual features of external brain morphology: the olfactory bulbs are located on stalks (the olfactory peduncles), rostral to the rest of the brain, and the sylvian fissure appears to be open (fig. 5). The pedunculate olfactory bulbs are the expected result of extremely large body size, an extension of the trend seen in modern prosimians where olfactory bulbs are more tucked under the frontal lobes in smaller species and extend

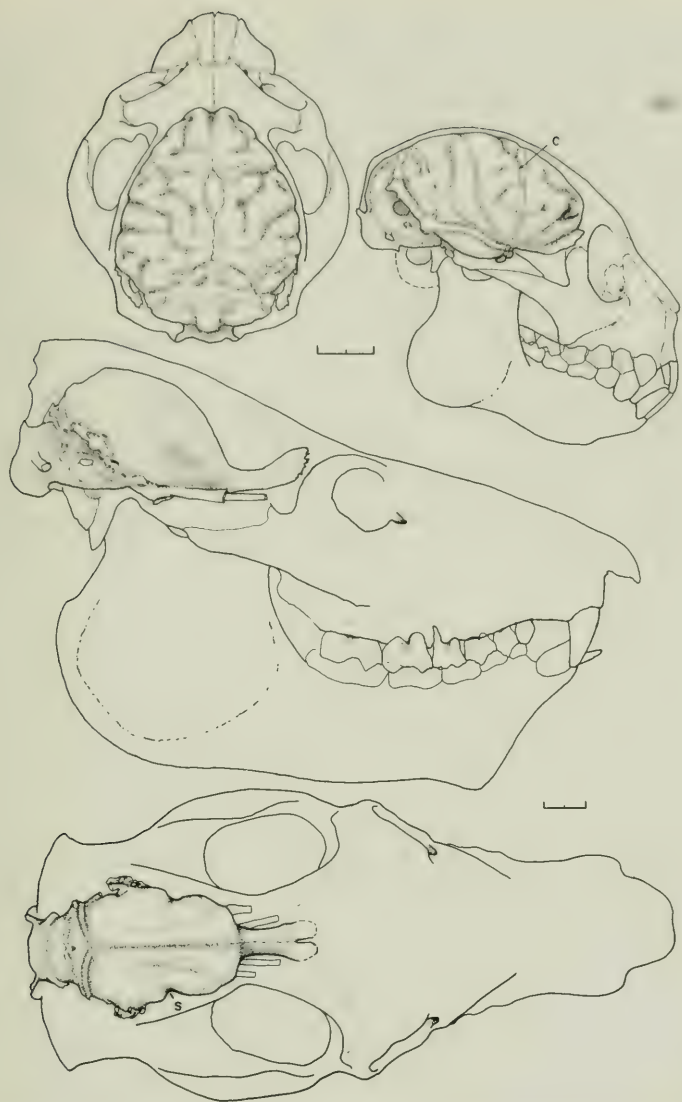


FIG. 5. Endocrasts and skulls of short and long-faced extinct giant lemuroids, to show differences in brain shape. Above, *Archaeolemur majori* (c = central sulcus); below, *Megaladapis edwardsi* (s = open sylvian sulcus). See text for discussion. Scales = 2 cm. (from Radinsky, 1970).

out more rostrally in their larger relatives (cf. figures in Radinsky, 1968). The main reason for this trend is the negative allometry of brains (i.e., brains are relatively smaller in larger species), which results in the brain occupying less of the space between face and occipital condyles in large forms. The olfactory bulbs must remain immediately behind the cribriform plate, which is at the back of the facial portion of the skull, and therefore they come to lie rostral to the frontal pole of the cerebrum. The open sylvian fissure may reflect the relatively small size of the brain compared with the skull and the lack of large orbits impinging on the brain rostrally. The only modern primate in which the orbits do not impinge on the frontal lobes is *Daubentonia*, and it also has an open sylvian fissure (Radinsky, 1968). Extrapolating from trunk length/body weight relationships in modern prosimians, Jungers (1978) estimated body weights of *Megaladapis grandidieri* and *M. edwardsi* to be 40 and 52 kg., respectively, with endocranial volumes of 85 and 138 cc., that yields relative brain sizes within the lower quarter of the modern prosimian range.

The short-faced giant lemuroids, like *Archaeolemur* and *Hadropithecus*, had relatively shorter and wider brains than did their long-faced contemporaries, with the olfactory bulbs tucked up against the front of relatively voluminous frontal lobes (fig. 5). The sulcal pattern differs from that of their small modern relatives (indriids) in being more wavy, and with more secondary sulci. The relatively globose shape is not what one would predict from simple allometric extrapolation from modern indriid brain shape. Rather, it suggests increased relative brain size in the extinct species over what exists in the modern indriids, with the more spherical shape reflecting having a larger brain relative to skull size (cf. modern anthropoids vs. similar-sized modern prosimians). The more wavy sulcal pattern, with more secondary sulci, in the giant extinct forms is expected, and conforms to trends seen in modern primates and ungulates, where larger forms have a more folded neocortex than their smaller relatives. This presumably reflects the fact that the neocortex increases in volume approximately isometrically with the rest of the brain, but is

organized as a thin sheet, and therefore must fold to be accommodated on the relatively decreasing amount of surface area/volume of the rest of the brain as brain size increases (Clark, 1947; Radinsky, 1975).

EARLY ANTHROPOID ENDOCASTS

The oldest known anthropoid endocasts are from the late Oligocene (about 27 my) of the Fayum region, Egypt. Incomplete endocasts of *Aegyptopithecus*, an early ape and a suitable ancestor for later apes and humans, reveal a lunate sulcus located more rostrally than in modern prosimians, and three additional transverse sulci, the most rostral of which is probably the central sulcus (fig. 6). The dorsal imprint of the olfactory bulbs suggest that they were relatively small. The brain appears to have been

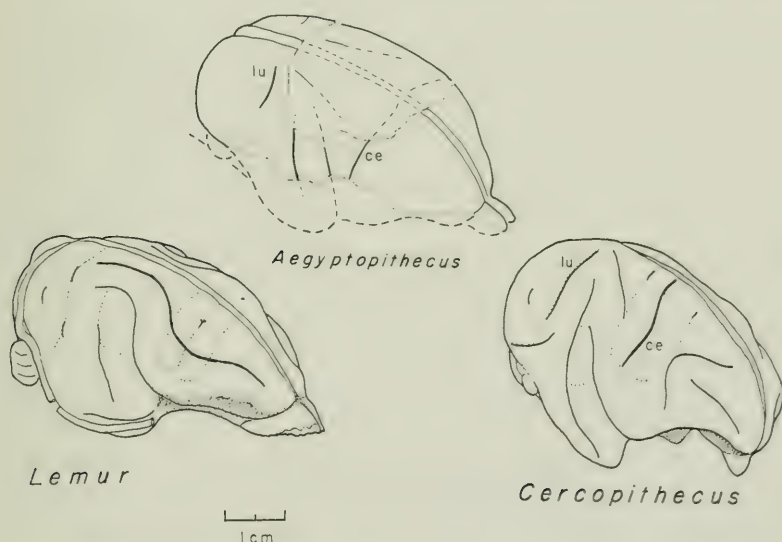


FIG. 6. Restoration of endocast of *Aegyptopithecus zeuxis*, compared with *Lemur variegatus* and *Cercopithecus talapoin* endocasts. Abbreviations: ce, central sulcus; lu, lunate sulcus. Dotted lines on modern endocasts delimit major functional areas (see fig. 1). All drawn to same scale.

relatively low and flat compared with the more spherical brains of most modern anthropoids, and the frontal lobe appears to have been relatively small.

The lunate sulcus bounds primary visual cortex in modern primates, and its relatively rostral position in *Aegyptopithecus* suggests expansion of that cortical area over the condition seen in most prosimians. The orbits of *Aegyptopithecus* do not appear to be relatively large, but comparative analysis, taking into account the affects of allometry, would be necessary to determine if they were larger than one would expect in a prosimian skull of that size.

A central sulcus is present in modern anthropoids but is absent in most prosimians (pottos are the main exception). It separates primary somatic sensory from primary motor cortex, and the significance of its presence vs. absence is not obvious. The apparently relatively small olfactory bulbs may be deceptive (if the rest of the brain has enlarged). If the brain is not relatively larger in *Aegyptopithecus* than in modern prosimians (see discussion below), then it is likely that the olfactory bulbs were reduced in size compared with what is seen in modern prosimians and in insectivorans.

Expanded visual cortex, development of a central sulcus, and possible reduction in size of olfactory bulbs are features in which the brain of *Aegyptopithecus* was advanced over the condition seen in most prosimians. A primitive feature of the brain of *Aegyptopithecus* was the relatively small frontal lobe (measured either from the sylvian fissure or the central sulcus, and compared with the rest of the brain), which lacks sulci (at least the sulcus rectus) that would be seen on frontal lobes of modern anthropoid brains of that size. The relatively low and flat brain shape is like that of large modern prosimians, and unlike the more spherical brain shape of most anthropoids. That difference probably is a reflection of brain size compared with skull size. Relatively large brains are more spherical in shape, presumably a packaging phenomenon as seen in miniature vs. large dogs (Radinsky, 1973a), small monkeys vs. comparably sized prosimians (Radinsky, 1975), small vs. large prosimians (allometric

effect) (Radinsky, 1968). If that interpretation is correct, it suggests that *Aegyptopithecus* had a relatively small brain compared to that of modern anthropoids (*contra* Radinsky, 1973b, 1974, based on foramen magnum comparisons). The only modern anthropoid with a brain shape like that of *Aegyptopithecus* is *Alouatta*, the howler monkey, which has the lowest relative brain size of any living anthropoid. From molar tooth size, Gingerich (1977) estimated body weight of *Aegyptopithecus* to be between 4.5 and 7.5 kg. The restored endocast suggests a brain volume of 27 to 32 cc., which results in a relative brain size falling below the modern anthropoid range, and within the lower half of the modern prosimian range.

The only other Fayum primate for which endocranial anatomy is known is *Apidium*, also about 27 my, and possibly close to the ancestry of Old World monkeys. Unfortunately, only the frontal lobe and olfactory fossa are preserved (see Radinsky, 1974), and they provide no significant information.

The oldest New World record of anthropoid brains is an endocast of *Dolichocebus*, a late Oligocene (25-30 my) form from Argentina, and an approximate contemporary of *Aegyptopithecus* and *Apidium* (fig. 7). The apparent lack of sulci other than the sylvian fissure may be an artifact of poor preservation. The significant feature revealed by the *Dolichocebus* endocast is that the occipital lobe was expanded beyond the condition seen in modern prosimians, and similar to the condition seen in modern anthropoids (compare lateral profiles in fig. 7). This suggests expansion of visual cortex to the modern anthropoid condition in ceboids as well as in hominoids back between 25 to 30 million years ago, not long after their first appearance in the fossil record.

Returning to the Old World, an isolated primate frontal bone from the early Miocene of Napak, Uganda (approximately 19 my) has yielded an impression of a frontal lobe with a sulcus rectus and a superior precentral sulcus (fig. 8). Judging from its size and morphology, it is most likely that the frontal bone is from the tiny ape *Micropithecus clarki* (Fleagle and Simons, 1978). It indicates considerable expansion of the frontal lobe over the

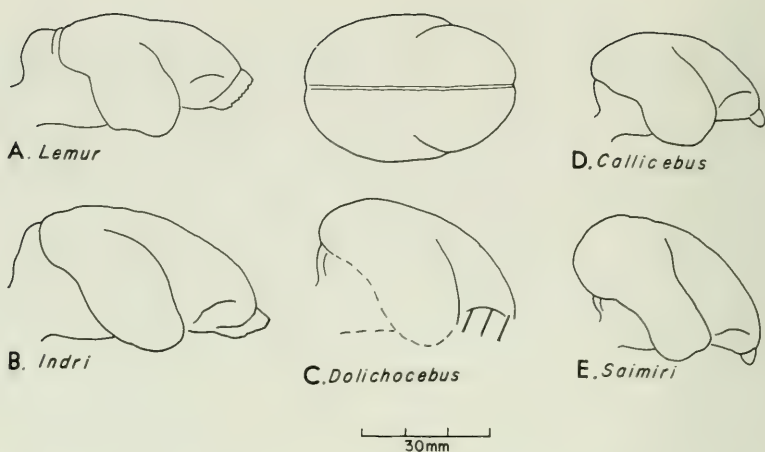


FIG. 7. Endocast of *Dolichocebus gaimanensis*, in dorsal and lateral views, compared with lateral views of endocasts of similar sized modern prosimians (left) and anthropoids (right), to show relative size of occipital lobe. Only the sylvian sulcus is indicated. All drawn to same scale (from Radinsky, 1974).

condition that existed 8 million years earlier in the larger ape *Aegyptopithecus* (cf. fig. 6). In fact, owing to the allometry of neocortical folding, one would not expect to see any more folding in the frontal lobe of a modern ape the size of *Micropithecus*. The frontal lobe of a modern cercopithecoid monkey the size of *Micropithecus* would have an arcuate sulcus caudal to the sulcus rectus (cf. *Cercopithecus*, fig. 8).

A partial endocast is known for another ape of approximately the same age as *Micropithecus*, but considerably larger in size: *Dryopithecus* (*Proconsul*) *africanus*, from 18-million-year-old (early Miocene) deposits in Kenya (fig. 9). The imprint of most of one cerebral hemisphere is preserved, and it reveals a sulcal pattern similar to that of the Napak specimen, with a superior precentral sulcus and a sulcus rectus (here with a short secondary spur) on the frontal lobe. The *Dryopithecus* sulcal pattern is similar to that seen in modern gibbons, except for the lack of a frontal lobe sulcus medial to the sulcus rectus. Since *D. africanus* was larger than a modern gibbon, that indicates less expansion of the frontal lobe in the Miocene form. The sulcal pattern of

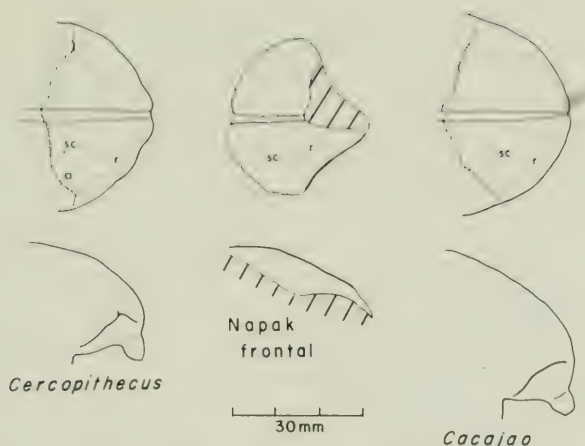


FIG. 8. Endocast from the Napak frontal, in dorsal and lateral views, compared with modern cercopithecoid (left) and ceboid (right) endocasts. The jagged line on the modern endocasts indicates the position of the frontoparietal suture. Abbreviations: a, arcuate sulcus; r, sulcus rectus; sc, superior precentral sulcus. All drawn to same scale (from Radinsky, 1974).

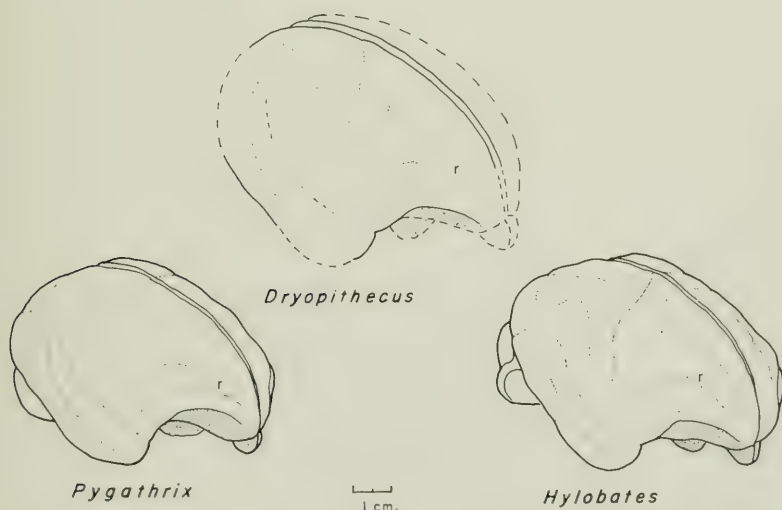


FIG. 9. Restoration of endocast of *Dryopithecus* (*Proconsul*) *africanus*, compared with endocasts of a modern cercopithecoid (left) and a modern hominoid (right). Abbreviation: r, sulcus rectus. All drawn to same scale.

Dryopithecus differs from that of modern Old World monkeys in lacking the arcuate sulcus. In 1974 I estimated the endocranial volume of *Dryopithecus africanus* at 150 cc. However, after reconsidering the crushed and incomplete nature of the endocast, I now believe that no reasonably accurate estimate of endocranial volume can be made from the specimen.

LATER ANTHROPOID ENDOCASTS

After *Dryopithecus*, only cercopithecids (Old World monkeys) and hominids are represented in the fossil record of anthropoid brain evolution. Although cercopithecids appear in the fossil record about 19 my, the oldest known endocast of this group is only 9 my, from the colobine *Mesopithecus*, from Pikermi, Greece. The *Mesopithecus* endocast (fig. 10) preserves the imprint of most of the cerebrum, and reveals a sulcal pattern indistinguishable from those seen on modern colobine endocasts. (Note in particular the arcuate-rectus sulcal complex, and compare with the condition seen in *Dryopithecus*). Among modern cercopithecids, brains of cercopithecines appear to be more advanced than those of colobines in several features (Falk, 1978), and it would be interesting to know when the cercopithecine condition was attained. Unfortunately, the oldest cercopithecine endocast is only 2 my. It is from *Paradolichopithecus arvernensis*, from the Villafranchian early Pleistocene of France, and as expected for such a late specimen, it shows in preserved portions the modern cercopithecine condition (Radinsky, 1974).

The fossil record of hominid endocasts consists of several specimens of small and large *Australopithecus* species (between 1 to 3 my), and of extinct *Homo* species. Unfortunately, they preserve little or no impressions of the cerebral convolutions, and we are left with information primarily on size and gross shape. Holloway (1975, 1976) concluded that *Australopithecus* endocasts (fig. 11) resemble those of modern humans and differ from those of chimps and gorillas in having greater relative height, more voluminous temporal lobes, a more horizontal orbital surface of

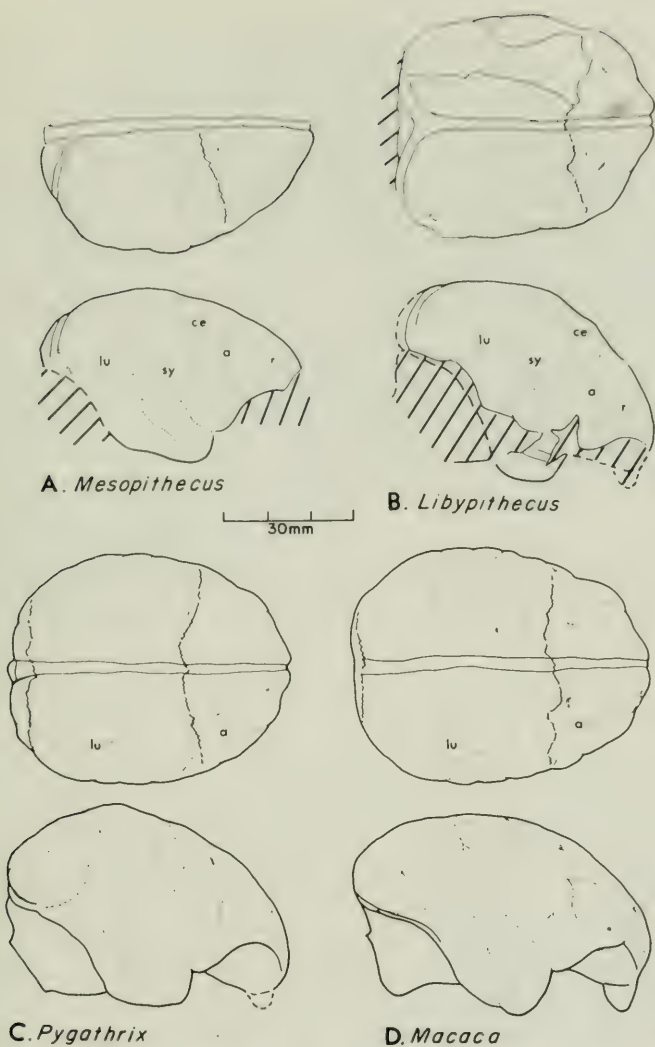


FIG. 10. Endocasts of extinct (above) and modern (below) Old World monkeys, in dorsal and lateral views. A, *Mesopithecus pentelici*; B, *Libypithecus markgrafi*; C, *Pygathrix nemaeus*, a modern colobine; D, *Macaca mulatta*, a modern cercopithecine. Abbreviations: a, arcuate sulcus; ce, central sulcus; lu, lunate sulcus; r, sulcus rectus; sy, sylvian sulcus. All drawn to same scale (from Radinsky 1974).



FIG. 11. Right lateral view of the Taung infant endocranium and face. Courtesy of Ralph L. Holloway.

the frontal lobe, and an apparently more caudally located lunatic sulcus. Relative brain size in *Australopithecus* is difficult to estimate, owing to insufficient evidence of body weight. Endocranial volumes of *A. robustus* and *A. africanus* average about 530 cc. and 440 cc., respectively (Holloway, 1975), and body weight estimates generally average around 40 to 50 kg. for the larger species and 30 to 35 kg. for the smaller (e.g., Pilbeam and Gould, 1974; McHenry, 1975). Those data suggest that relative brain size in *Australopithecus* was above the observed range of modern apes and monkeys, but considerably below that of modern humans.

Holloway (1975, 1976) has hypothesized that the resemblances between endocranial casts of *Australopithecus* and *Homo*, and in particular the inferred relatively caudal position of the lunatic sulcus, indicate cortical reorganization to a human pattern in *Aus-*

tralopithecus. However, the caudal displacement of the lunate sulcus, presumed to reflect expansion of the parietal association cortex, is suggested only by blurred gyral impressions on one specimen (the Taungs endocast). From that evidence, I see a relatively caudal position of the lunate sulcus as possible but not necessarily probable (it may have been more rostrally located). The differences in shape of *Australopithecus* vs. chimp and gorilla endocasts may be a packaging phenomenon, reflecting the greater relative brain size of *Australopithecus*. In any event, even if new material confirms the suggestion of a caudally displaced lunate sulcus in *Australopithecus*, I do not see that feature, plus the shape differences, as sufficient evidence for the conclusion that the brain of *Australopithecus* was reorganized to a human pattern, or was significantly more human-like than ape-like in terms of functional capabilities. The only concrete evidence we have of significant divergence from the modern anthropoid brain condition in *Australopithecus* is the increased relative brain size, and in that feature *Australopithecus* is about one-half of what one would expect in a modern human brain.

Endocasts of extinct species of *Homo* have been analyzed primarily with respect to gross size (e.g., Lestrel, 1975), although attempts have been made to define and infer significance of apparent changes in size and shape of various parts of the endocast (e.g., LeMay, 1976; Kochetkova, 1978; Holloway, in prep.). Owing to the lack of impressions of cerebral convolutions on fossil hominid endocasts, I see brain size as the only data we can be sure of. Endocasts of *Homo erectus*, from between 0.5 to 1.0 my, average about 930 cc. in volume (Holloway, 1975), which is about 70 percent the size of modern human brains. Unfortunately, lack of information on body weights precludes refined analysis of changes in relative brain size.

EVOLUTIONARY TRENDS

Quantitative studies show that the brains of modern primates differ from those of insectivorans (representative of the primitive

placental condition) in being relatively larger compared with body size, and in having relatively more neocortex (beyond what one would expect from the increased brain size), an expanded visual system, and a reduced olfactory system (Stephan, 1969; Stephan, Bauchot and Andy, 1970). Brains of modern anthropoids differ from those of modern prosimians in being more derived (i.e., further removed from the primitive condition) in those features, and also in having the primary motor and somatic sensory cortices divided by a transverse central sulcus instead of having head and postcranial body representations in those areas separated by a longitudinal coronal sulcus (see fig. 1). There may be major differences indicative of evolutionary trends in other systems, such as auditory, somatic sensory, or motor, and we await the quantitative comparative studies needed to investigate those possibilities.

The fossil record of primate endocasts suggests that expansion of neocortex in general, expansion of visual cortex, and possibly also reduction of olfactory bulbs had begun by 55 million years ago, at the beginning of the second evolutionary radiation of primates. Endocasts of some of the oldest known anthropoids suggest that by 25 to 30 million years ago, expansion of visual cortex and reduction in olfactory bulb size had progressed further, and was within the modern anthropoid range. Further, the *Aegyptopithecus* endocast reveals that the central sulcus had appeared by that time, at least in Old World anthropoids. In both anthropoids and prosimians, expansion of frontal lobes lagged behind that of the rest of the brain.

Reliable estimates of relative brain size are not available for most fossil primate endocasts. It is likely that in the early (55 to 35 million years old) prosimians, relative brain size was below the modern prosimian average, and in some of the early forms (*Tetoniaus*, *Smilodectes*, *Adapis*), may have fallen below the range of modern prosimians. It also is likely that relative brain size in *Aegyptopithecus*, one of the oldest known anthropoids, fell below the range of modern anthropoids, and was within the lower half of the modern prosimian range. We do not know when modern relative brain sizes were attained by prosimians and anthropoids,

but endocasts that are modern in general appearance are known for both groups by about 18 million years ago (*Komba* and *Dryopithecus*).

Brains of modern humans average about 3 to 3.5 times as large as one would expect in a modern anthropoid of our body size, and many of the unusual features of our brain (extraordinarily expanded and highly folded neocortex, large neocortical association areas, large cerebellum) may be results of our unusually large brain [Radinsky, 1975]. The fossil record of hominid endocasts suggests that the increase in relative brain size above the normal anthropoid range had begun by 2 to 3 million years ago (seen in *Australopithecus*), and that the modern condition was attained only within the past half-million years (after *Homo erectus*).

OUTSTANDING QUESTIONS

Some of the trends seen in the fossil record of primate brain evolution can be interpreted functionally, at least in a very general way. Expansion of visual cortex and reduction in size of olfactory bulbs suggests increased importance of vision and decreased importance of olfaction in the way of life of the animals under consideration. However, what that means more specifically cannot be inferred at this time. We need more information of two kinds: experimental evidence of the functional significance of major differences in size of visual and olfactory systems, and more extensive behavioral observations of species in the wild, comparing those with relatively small vs. relatively large visual and olfactory systems.

Other trends in primate brain evolution cannot be interpreted at this time, even in a general way. These include development of a central sulcus in anthropoids (and a few prosimians), expansion of frontal lobes, and increase in relative brain size. Insights into the first two might be obtained from comparative quantitative analyses (does frontal lobe size scale allometrically? are the primary motor and somatic sensory strips broader [rostrocaudally]

in primates with a central sulcus?). The last, increase in relative brain size, is an evolutionary trend of particular interest, for it occurred in many other groups of mammals (see e.g., Jerison, 1973; Radinsky, 1978), and was carried to a unique extreme relatively recently in humans. It is commonly believed that relative brain size is correlated with intelligence, and that intelligence has important survival value. However, there is surprisingly little scientific evidence demonstrating a relationship between brain size and intelligence. It is difficult to devise experiments that compare intelligence in different species, with brain size isolated as the critical variable, and it is not clear how abilities tested in the lab relate to abilities used in the wild. Further, and related to the last point, I know of no evidence that shows a relationship between intelligence, however one defines it, and fitness (increased reproductive probability). Elucidation of the factors responsible for the widespread evolutionary trend of increase in relative brain size in mammals, and for the extreme to which that trend was carried in humans, remains a fascinating unsolved problem.

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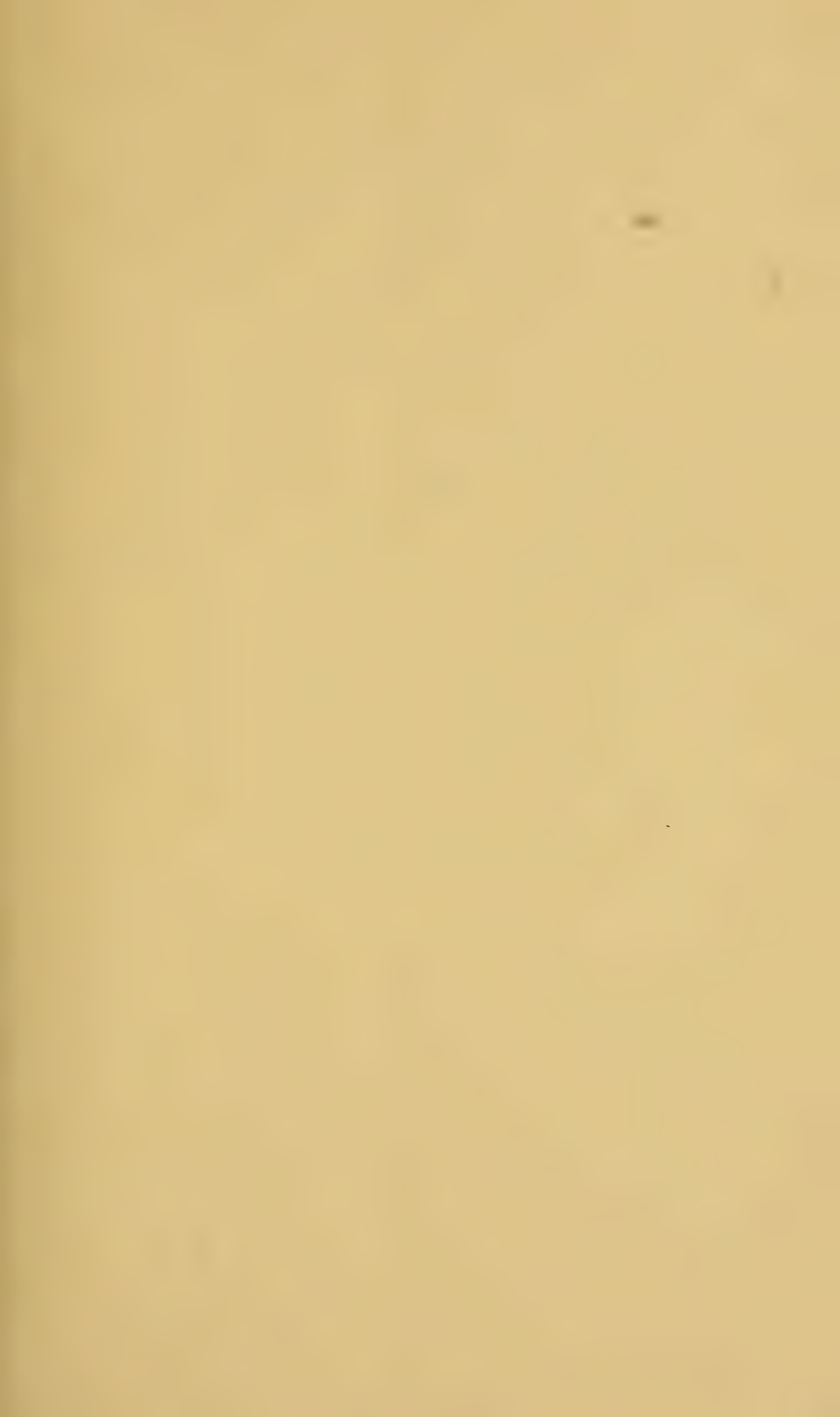
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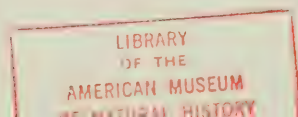
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†Published version: *The Brain in Hominid Evolution*, New York: Columbia University Press, 1971.

HUMAN BRAIN EVOLUTION IN AN ECOLOGICAL CONTEXT

INTRODUCTION

Several previous James Arthur Lectures have dealt with the question of overall brain size and morphology in human evolution (Harman, 1956; Tobias, 1971; Holloway, 1973a; Radinsky, 1979), considering the question from a variety of different angles. It is by now well established (see Gould, 1966, 1975; Jerison, 1973) that any discussion of brain size in evolution must be accompanied by appropriate reference to body size, taking into account any effects of *allometric scaling*. In overall evolutionary terms, reference to the absolute size of the brain alone is of little value, and if scaling of the brain to body size is found to be non-linear (i.e., *allometric*, as opposed to *isometric*), use of simple ratios is equally uninformative. Many studies have now revealed that various biological parameters of vertebrate groups (e.g., brain size in mammals) scale allometrically with body size and there is widespread use of the *empirical allometric formula*:

$$Y = k \cdot X^{\alpha}$$

to describe the overall relationship between any given parameter (Y) and body size (X). In its logarithmic form, this equation becomes linear:

$$\log Y = \alpha \cdot \log X + \log k$$

and it is a relatively simple matter to determine a best-fit straight line for any set of logarithmically transformed data. This permits inference of values for the allometric exponent (α) and for the allometric coefficient (k). There is still some controversy over which line-fitting technique to use for determining allometric relationships and varying use has been made of the three best known techniques: regression, reduced major axis and major axis. For reasons discussed elsewhere (Pilbeam and Gould, 1974; Harvey and Mace, 1982; Martin, 1982) the major axis is used throughout the present paper. In some cases, it is found that logarithmically transformed data for

paired values of a given parameter (e.g., brain size and body size) fit a single straight line fairly closely, and where the correlation coefficient (r) is high it makes little difference which line-fitting technique is employed. In other cases, however, it is found that the data show wide scatter and the choice of best-fit line then affects the conclusions drawn. Finally, it is commonly found that the data fit two or more separate lines (characteristically with closely similar slopes) of differing elevation, as shown in figure 1. In such cases, one can recognize the existence of different *grades* in the allometric relationship between the selected parameter and body size (Martin, 1980). When the data are derived exclusively from living species, the recognition of distinct grades is relatively unproblematic, though a certain degree of subjectivity in interpretation may be involved. However, caution must be exercised when relationships are determined for fossil forms. As pointed out previously (Martin, 1980), description of an allometric relationship for a time series of fossil forms approximating an evolutionary sequence ("phylogenetic allometry"—see Gould, 1966) may be of little value, since this combines the two phenomena of a grade-shift through time and phylogenetic change in body size. For instance, in hominid evolution it happens to be the case that there has been an overall trend toward increase in body size as well as a trend in increased brain size, and the high slope value obtained by fitting a best-fit line to brain and body size data for a time sequence of hominid fossils (e.g., Pilbeam and Gould, 1974) results from the combination of these two trends (see fig. 1). If in human evolution the trend toward increased brain size had been combined instead with a gradual *decrease* in body size over time (phyletic dwarfing), a *negative* slope value would have been obtained despite the enhancement of relative brain size. Failure to separate the effects of phyletic size change from allometric scaling effects has been a major source of confusion in discussions of size-related characters in human evolution.

Proper application of allometric analysis to quantifiable characters such as brain size permits effective comparison of large numbers of species of widely differing body sizes. This greatly increases the generality of any conclusions which may be drawn and avoids the common problem encountered in studies of human evolution where

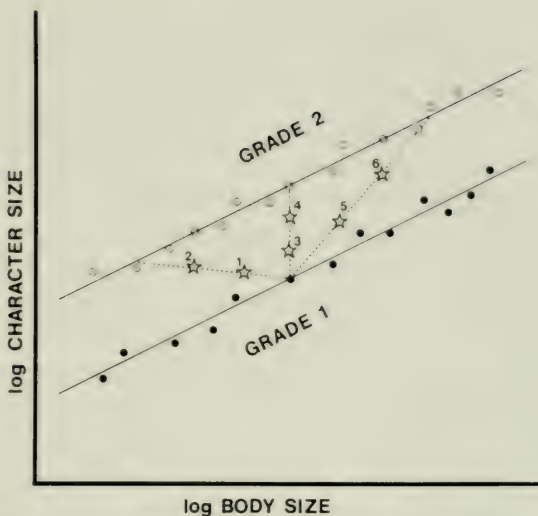


FIG. 1. The concept of allometric "grades." Species belonging to two separate grades (black circles = grade 1; open circles = grade 2) obey the same scaling principle, reflected in the common slope of the parallel straight lines. Grade shifts in the course of evolution involve vertical readjustment on the graph, relative to the scaling trend. When fossil forms (stars 1–6) are available to document such a grade-shift, fitting of best-fit lines confuses change in body size with vertical readjustment on the graph. Decrease in body size combined with an upward grade shift (stars 1 and 2) results in a negative slope value, while increase in body size (stars 5 and 6) produces a positive value and maintenance of constant body size (stars 3 and 4) would produce a value of infinity! [Diagram modified from Martin, 1980.]

far-reaching conclusions are drawn from a very restricted data base. There are now numerous examples, notably with respect to brain size : body size relationships, demonstrating the value of allometric analysis in the following areas:

1. Recognition of general scaling principles, as reflected by the empirically determined value of the slope (exponent α) for logarithmically transformed data plots.
2. Recognition of differential adaptations, where individual species (outliers) or entire groups of species (distinctive grades—fig. 1) separate out on the logarithmic data plot. Here, the empirically determined allometric relationship can be used as a basis for calculating indices reflecting the departure of individual species

- from an overall trend. Such indices have, for example, been calculated in various ways for mammals to provide a measure of relative brain size which effectively takes account of body size differences (e.g., "encephalization index" of Stephan, 1972; "encephalization quotient" of Jerison, 1973 and of Eisenberg, 1981).
3. Testing of specific hypotheses, by predicting scaling relationships for individual species from consideration of other evidence.
 4. Prediction of unknown values (or, simply, "expected" values) for species where the body size is known but the dimension of a particular parameter, such as brain size, may not be known in advance. This application may, of course, fall under the heading of hypothesis-testing as well.
 5. Inference of functional relationships from empirically determined patterns of allometric scaling. The manner in which a given parameter varies with body size, following some recognizable scaling principle, may suggest underlying functional processes. However, it must be emphasized that allometric analysis is a purely *empirical* procedure and that any hypotheses generated from the results must be subjected to detailed scrutiny using other evidence before the *correlations* recognized can be confidently linked to underlying *causal relationships* (see later).

APPLICATION OF ALLOMETRIC ANALYSIS TO THE EVOLUTION OF THE HUMAN BRAIN

In the following discussion, the basic concepts of allometric analysis are applied in a number of different ways in order to identify special features of human brain evolution. Wherever possible, the comparisons involved will be as broad as available data permit in order to place *Homo sapiens* in perspective among his closest relatives, the primates, and indeed among the placental mammals generally. In some cases, the allometric relationships concerned involve an analysis of the typical adult condition for a wide range of species (*interspecific allometry*), whereas in others developmental aspects within individual species (*ontogenetic allometry*) are considered. In all instances, however, the common goal will be to identify what is

so special about the size of the human brain (including its ontogenetic development to reach that size) and to extract clues which indicate possible ecological factors that have promoted the emergence of a particularly large brain during human evolution. In doing this the evolution of the human brain will be examined from a somewhat unusual standpoint. Numerous research workers, including a large proportion of previous lecturers in the James Arthur Lecture series, have concerned themselves with determining, at various levels, how the human brain functions, and spectacular advances have of course been made in this domain. Other investigators have sought explanations for the large size of the human brain in terms of specific selection pressures, such as the requirements of increasing complexity of social life (Holloway, 1973a). In other words, they have asked why human beings should have *needed* increasingly large brains in the course of their evolution. But there is a third approach which may be taken, which is specifically relevant in ecological terms. It is well known that the human brain (especially the gray matter—Thews, 1960) requires a great deal of energy both for its development and for its maintenance (e.g., see Armstrong, 1982a). For instance, in the adult human being the brain represents only about 2 percent of body weight, yet it consumes some 18 percent of the body's energy (Lazorthes et al., 1961—cited in Blinkov and Glezer, 1968). One might therefore ask how, in energetic terms, human beings can support such an exceptionally large brain and how, in the course of human evolution, additional energy was made progressively available to meet the needs of an ever-increasing brain size. This is the question that will be asked in the following pages and, as might be expected from a somewhat unusual approach, some rather unexpected answers will be seen to emerge.

SCALING OF BRAIN SIZE IN PRIMATES AND OTHER MAMMALS

There is now a substantial literature dealing with allometric analysis of brain size in mammals generally and in primates in particular (Bauchot and Stephan, 1966, 1969; Stephan, 1972; Jerison, 1973, 1977; Gould, 1975; Martin, 1981; Passingham, 1975, 1981; Szarski,

1980; Armstrong and Falk, 1982). Considerable success has been achieved in identifying separate grades of relative brain size among the mammals and in examining the brain size of individual species (such as man) in relation to some common baseline. Bauchot and Stephan, for instance (see Stephan, 1972) have taken the allometric relationship for relatively primitive members of the order Insectivora (families Soricidae, Tenrecidae, Erinaceidae) as a baseline against which to compare other mammals, following the rationale that relative brain size in these insectivores represents a minimal condition for modern mammals. The relative enlargement of the brain in other mammals can be expressed as an encephalization index ("index of progression"), using the empirical formula determined for the allometric relationship between brain size (E, in mg) and body size (P, in g) in "basal insectivores":

$$\log_{10} E = 0.63 \cdot \log_{10} P + 1.63 \quad (1)$$

Calculation of the index value for any individual mammal species simply amounts to dividing the actual brain size of that species by the "expected" value predicted from the basal insectivore equation for the body size concerned. This can be illustrated (fig. 2) by plotting best-fit lines for the relationships between cranial capacity and body weight for the following 4 "grades":

1. "basal" insectivores (hedgehogs, shrews, and tenrecs)
2. "advanced" insectivores (moles, desmans, elephant-shrews, tree-shrews, etc.)
3. strepsirhine primates (lemurs and lorises)
4. haplorhine primates (tarsiers, monkeys, and apes).

[N.B. Cranial capacity in cc. is approximately equivalent to actual brain weight in g, at least for insectivores and primates, and the two measures of brain size are therefore used interchangeably in the following text, though actual brain weight is used wherever possible.] As shown by Bauchot and Stephan for actual brain weights (1969; see also Stephan, 1972), the best-fit lines through these four grades all have similar slopes. Major axes fitted to the data in figure 2 have slopes averaging 0.68 (range: 0.62–0.75). Compared with the basal insectivore line, advanced insectivores typically have brains twice

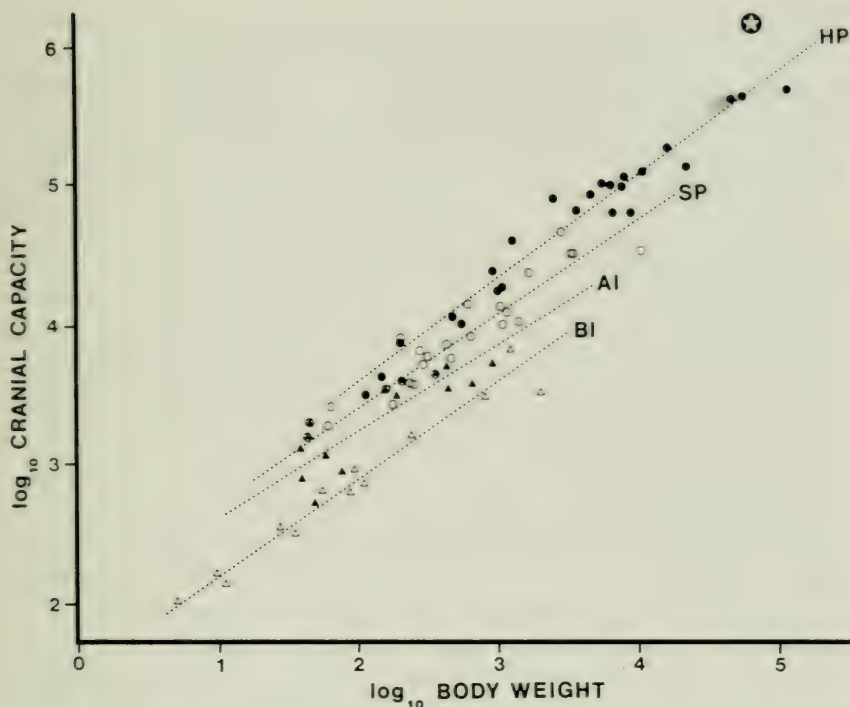


FIG. 2. Logarithmic plot of cranial capacity (C, in mm³) against body weight (P, in g) for:

- (i) "basal" insectivores (BI): open triangles (N = 13)

$$\log_{10}C = 0.68 \cdot \log_{10}P + 1.51 \quad (r = 0.98)$$

- (ii) "advanced" insectivores (AI): black triangles (N = 15)

[N.B. Black triangles for five tree-shrew species surrounded by circles.]

$$\log_{10}C = 0.62 \cdot \log_{10}P + 1.99 \quad (r = 0.94)$$

- (iii) strepsirhine primates (SP): open circles (N = 22)

$$\log_{10}C = 0.68 \cdot \log_{10}P + 2.07 \quad (r = 0.94)$$

- (iv) haplorhine primates (HP): black circles (N = 25)

$$\log_{10}C = 0.75 \cdot \log_{10}P + 2.07 \quad (r = 0.97)$$

Homo sapiens (not included in haplorhine best-fit line calculation) shown by white star in black circle. Best-fit lines are major axes.

Cranial capacities are based on average measurements for eight skulls (wherever possible) of each species, using sintered glass beads. Body weights are taken from the literature (Stephan, Bauchot, and Andy, 1970; Rudder, 1979; Eisenberg, 1981).

as big, strepsirhines typically have brains almost four times larger, and haplorhines as a group have brains seven times larger. *Homo sapiens* has a brain size about 20 times larger than would be expected for a basal insectivore of the same body size (if such a creature were to exist) and obviously stands out in relation to haplorhine primates, having a brain size about three times larger than typical haplorhines (such as the great apes). Incidentally, figure 2 also shows that the great apes (chimpanzee, gorilla, orang-utan) follow the common haplorhine pattern; although the great apes do have larger brains than monkeys, this can be attributed simply to their larger body size. *Homo sapiens*, by contrast, clearly is more advanced than both monkeys and apes in terms of relative brain size.

An alternative approach to calculating an index of relative brain size has been pioneered by Jerison (1973), who selected as his base-line the *typical* condition for modern mammals, rather than the *minimal* condition. Jerison's "encephalization quotient" is based on an overall best-fit line for mammals, which he expressed by the following formula (converted to the units used throughout this text):

$$\log_{10}E = 0.67 \cdot \log_{10}P + 2.08 \quad (2)$$

(As before, E = brain weight in mg; P = body weight in g.) On this basis, *Homo sapiens* has an encephalization quotient value of 6.3, indicating that modern man has a brain size just over six times bigger than would be expected for a "typical" mammal lying directly on the best-fit line (Jerison, 1973). In practice, there is little difference between the encephalization index of Bauchot and Stephan (Stephan, 1972) and Jerison's encephalization quotient, since the values taken for the allometric exponent (α) are very similar (0.63 vs. 0.67). Hence, Jerison's quotient values for individual species are approximately one-third of the index values given by Bauchot and Stephan's formula.

Recently, however, a fundamental problem has arisen with respect to the best-fit line for brain : body size relationships in mammals. Jerison (1973) followed a long tradition in accepting the value for the allometric exponent (α) as 0.67 and in fact assumed this value to be correct in determining his allometric equation for calculating encephalization quotient values (see also Pilbeam and Gould, 1974).

Statistical analysis of markedly larger samples of data for mammal species has now shown the exponent value to be closer to 0.75 (Bauchot, 1978; Eisenberg, 1981; Martin, 1981; Hofman, 1982). Eisenberg and Redford (see Eisenberg, 1981) determined the following empirical formula for a sample of 547 mammal species, including marsupials:

$$\log_{10}E = 0.74 \cdot \log_{10}P + 1.74 \quad (3)$$

[Converted to give units as for equation (1) above.]

Similarly, Martin (1981) determined the following formula for a sample of 309 placental mammals (see fig. 3):

$$\log_{10}E = 0.76 \cdot \log_{10}P + 1.77 \quad (4)$$

In the latter case, the 95 percent confidence limits on the exponent value obtained from the slope of the major axis (0.73–0.78; $r = 0.96$) were found to exclude the previously accepted value of 0.67. This obviously has implications both for determination of indices derived from the allometric relationship and for hypotheses regarding the functional significance of relative brain size. In fact, all the potential applications of allometric analysis listed above depend upon the empirical values determined for the relationship between brain size and body size in mammals. It is therefore important to establish a fairly conclusive allometric formula for the mammals.

One justification for accepting the higher value of approximately 0.75 for the allometric exponent in the mammalian brain : body size equation (e.g., fig. 3) is that all analyses involving really large samples of mammal species (N greater than 240) agree in producing exponent values closer to 0.75 than to 0.67. The data set compiled by Crile and Quiring (1940), which has been widely used by previous authors (including Jerison, 1973) and which does actually yield an exponent value close to 0.67 (Martin, 1982), included only 97 mammal species and did not provide a representative selection of mammals (notably at the upper end of the body size range). Nevertheless, it might be argued from an examination of figure 3 that the exponent value determined for the much larger sample of 309 mammal species is biased by the preponderance of relatively small-brained species at

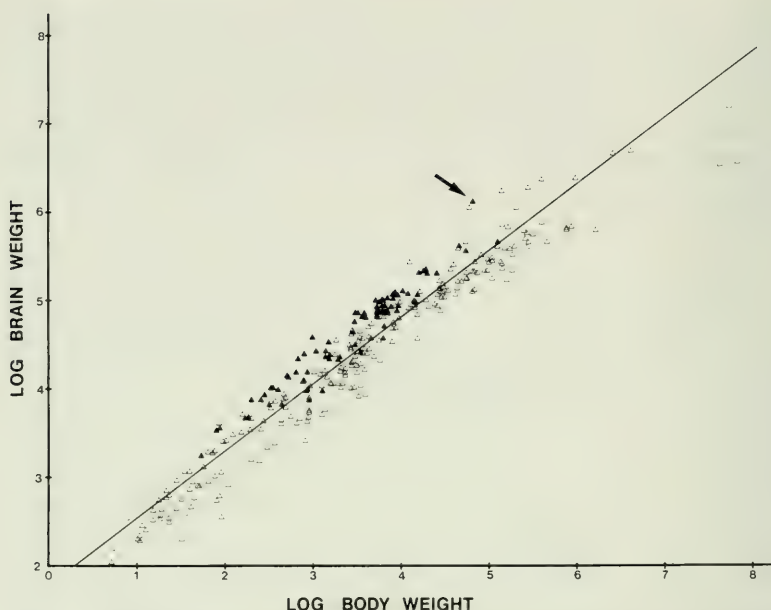


FIG. 3. Logarithmic plot of brain weight (E, in mg) against body weight (P, in g) for a sample of 309 placental mammal species. Open triangles = non-primates; black triangles = primates; arrow indicates *Homo sapiens*. Best-fit line is the major axis. (From Martin, 1981, reprinted by permission from *Nature*, vol. 293, no. 5827, pp. 57-60. Copyright © 1981 Macmillan Journals Ltd.)

the lower end of the graph (though the small-brained whales at the other end would surely counterbalance this, to some extent at least). In order to remove any preponderant influence of one large group of mammals falling into a particular grade of relative brain size, the allometric equation was recalculated for the data in figure 3 by taking the average values for $\log_{10}E$ and $\log_{10}P$ for each of the 10 orders of placental mammals represented. As shown in figure 4, these average values show a very clear straight line relationship, with a very high correlation coefficient ($r = 0.993$) and a slope close to 0.75:

$$\log_{10}E = 0.78 \cdot \log_{10}P + 1.61 \quad (5)$$

The 95 percent confidence limits of the slope of the major axis (0.72-0.84) once again exclude the value of 0.67 as being too low. It is also interesting to note that this analysis does reveal that the primates

are somewhat distinctive as an order in terms of the overall expression of relative brain size (fig. 4), whereas this is not obvious from a plot of individual species (fig. 3) because of the considerable variability within orders of mammals and overlap between them when values for individual species are plotted. In any event, the evidence suggests that the correct value for the empirically determined allometric exponent governing brain : body size relationships in placental mammals is not 0.67 but significantly higher than that, in the region of 0.75.

There is, however, another major problem involved in identifying exponent values for brain : body size relationships in mammals. It is a well-known fact (e.g., see Pilbeam and Gould, 1974; Gould, 1975; Mace, Harvey, and Clutton-Brock, 1980) that the exponent value tends to decrease with decreasing level of the taxonomic unit examined. Whereas a value close to 0.75 seems to be appropriate for the eutherian mammals overall, individual orders or suborders of mammals tend to yield lower exponent values (e.g., fig. 2) and average exponent values usually decrease further as even lower taxonomic levels (e.g., families; subfamilies; genera) are considered, with the lowest values of all obtained with comparisons of adult individuals of a single species (*intraspecific allometry*). The reasons for this phenomenon remain obscure, though a theoretical explanation may ultimately emerge (e.g., see Martin and Harvey, in press). In practice, this variation in exponent value with taxonomic level means that the conclusions reached may vary with the level at which allometric analysis is conducted, leading to a certain degree of subjectivity and confusion (as was recently aptly pointed out with respect to hominid evolution by Holloway and Post, 1982). Of course, until we understand why exponent values vary in this way, it will remain difficult to decide which is the "correct" value to take in a given situation; but two pragmatic guidelines recommend themselves:

1. The exponent values used should be appropriate to the particular comparisons involved. For instance, in comparing strepsirhine primates with haplorhine primates (fig. 2), we should use allometric equations which are derived from analyses of these two major subgroups of the order primates.



FIG. 4. Average values for logarithms of brain weight (E, in mg) and body weight (P, in g) for 10 orders of placental mammals (circles), with the best-fit line (major axis). Marsupials (M in diamond) actually lie quite close to the best-fit line for placentals. Ungulates (U) are treated as a single order; separate values for artiodactyls do not affect the results of the analysis.

Key:

B = bats (Chiroptera)

I = insectivores (Insectivora), including tree-shrews

R = rodents (Rodentia)

L = rabbits and hares (Lagomorpha)

E = edentates (Edentata)

P = primates (Primates)

C = carnivores (Carnivora)

U = hoofed mammals (Ungulata)

S = seals and sea-lions (Pinnipedia)

D = dolphins and whales (Cetacea)

Note that the average value for primates (arrowed) lies highest relative to the line, indicating a greater emphasis on large brain size in the order Primates overall.

(N.B. an independent regression analysis conducted at the order level by Armstrong, 1982b on 93 mammal species belonging to 16 orders yielded an exponent value of 0.72; $r = 0.95$).

2. Since at least part of the variation in exponent value with taxonomic level is due to statistical side-effects of decreasing sample size (Martin and Harvey, in press), comparisons should be conducted at the highest possible taxonomic level, wherever there is

a choice, in order to include a maximum number of species and a maximal range of brain and body sizes.

These two guiding principles are used consistently in the following discussion.

FUNCTIONAL INTERPRETATION OF BRAIN SIZE SCALING IN MAMMALS

As long as it was generally accepted that brain size scaled to body size with an exponent value of 0.67 in mammals and in other vertebrates, it was logical to seek some explanation of brain size scaling in terms of surface : volume relationships, which are governed by an exponent of the same value. Indeed, Jerison (1973, p. 49) specifically comments on this possibility: "We should note that an exponent of $\frac{2}{3}$ implies a surface : volume relationship and may, therefore, be the basis for theorizing on the significance of brain size." But now that there is good evidence that the exponent value for mammals is considerably higher than 0.67, some alternative explanation of the significance of brain size scaling relationships must be sought. One immediate possibility that presents itself is a link between relative brain size and metabolic turnover. It has been known for some time (Kleiber, 1932, 1947, 1961; Brody, 1945) that basal metabolic rate in mammals and other vertebrates (viz., the quantity of oxygen consumed, or of calories produced, in a standard time at rest) scales to body size with an exponent value of approximately 0.75 ("Kleiber's Law"). More recently (Mace and Harvey, 1982), it has been shown for a sample of mammals and birds that *active* metabolic rate (i.e., total metabolic turnover, including energy spent in activity, over a standard time) also scales in a negatively allometric fashion. The coincidence between the exponent values for basal metabolic scaling and brain size scaling might, therefore, reflect some underlying functional relationship between them. In fact, even in the absence of an adequate sample size for brain and body weights in mammals, Brody (1945, p. 619-622) had already suspected the possibility of such a link:

for mature mammals of different species, the basal heat production increases with the 0.73 power of body weight; the brain weight increases with the 0.70 power of body weight, virtually the same as for basal heat production. . . . The most conspicuous feature is that the slope of the curve relating brain weight to body weight is virtually the same as the slope relating basal heat production to body weight. . . . Does this close *statistical* correlation imply the presence of a similarly close *causal physiological* interrelation between organ weight and metabolism? It may be so. It is known that the blood supply to the brain—about 13 percent of the cardiac output (Barcroft and others)—is all out of proportion to the relative weight of the brain. Kestner (1935, 1936) estimated that under basal metabolism conditions nearly half of the blood passes through the brain. Hence Kestner's conclusion that under basal metabolism conditions the brain probably conditions the level of basal metabolism. [N.B. Kestner had, in fact, overestimated.]

This prophetic train of thought in fact also underlines one of the major problems involved in proceeding from the results of allometric analysis to inference of functional relationships. It must first of all be established that the similarity of exponent values in metabolic scaling and brain size scaling in mammals is more than a coincidence and reflects some real causal relationship. But it must also be established that this causal relationship operates in a particular direction. Brody's implied suggestion (above) that control of body metabolism depends upon brain size, which was echoed by other authors, has now been largely discredited; but Brody did not mention the alternative interpretation that brain size is instead constrained by the metabolic turnover of the body. This alternative possibility has now been explicitly proposed by Martin (1981) and by Armstrong (1982a, 1982b) and provides an entirely different basis for interpreting brain size evolution in the vertebrates. Even here, there are at least two different hypotheses which can be recognized. The simplest is that an adult mammal requires a particular metabolic turnover to permit operation of its brain tissue, which is (as mentioned above) very expensive in energetic terms. However, this possibility seems unlikely for a number of reasons (Martin, 1981). An alternative hypothesis is that it is the mother's metabolic turnover which, both in direct terms (through the physiology of gestation) and in indirect terms (through the partitioning of resources between maintenance and reproduction), determines the size of the neonate's brain and hence the ultimate size of the adult brain. This latter hypothesis has generated a number of testable predictions, some of which are

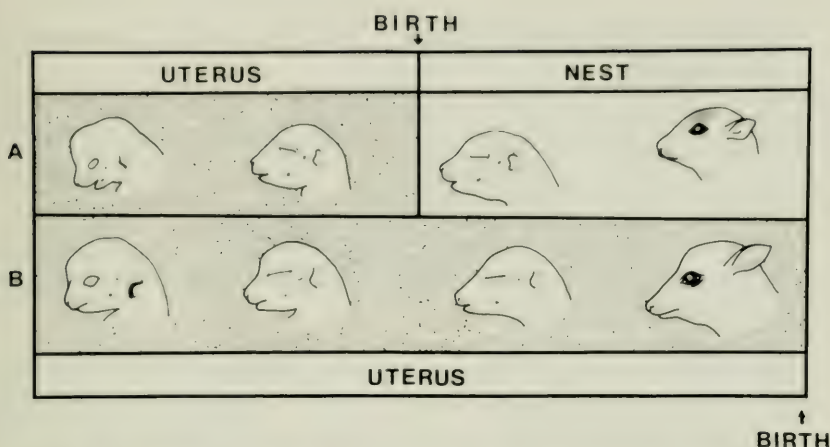


FIG. 5. Contrast between altricial mammals (A) and precocial mammals (B), adapted from Portmann (1962). The gestation period (indicated by stippling) is markedly longer, relative to body size, in precocial mammals compared to altricial species.

considered below, and provides a promising basis for the interpretation of brain size in mammals.

Obviously, if it is the mother's metabolic turnover which exerts a major constraining influence on the developing foetal brain, the size of the neonatal brain will also depend upon the length of the gestation period. For any given maternal body weight with a given metabolic turnover, an increase in gestation period should lead to (or at least permit) an increase in neonatal brain size. This expectation relates directly to a major distinction which can be made among mammals with respect to the state of the offspring at birth (Portmann, 1941, 1962). Once various allometric effects of the mother's body size (e.g., with respect to gestation period and neonate weight) have been taken into account, most mammal neonates can be classified into two major types (fig. 5):

1. *Altricial neonates*: Fairly large litters of small neonates born after a relatively short gestation period. Both brain and body weight are relatively small at birth, associated with a generally poor level of development (eyes and ears closed; no hair through; incomplete development of homeothermy, etc.). They grow into adults with

relatively small brains. [Examples: most insectivores, carnivores, and rodents.]

2. *Precocial neonates*: Small litters of large young (typically only a single neonate) born after a relatively long gestation period. Both brain and body weight are relatively large at birth, associated with a relatively advanced level of development (eyes and ears open; hair through; homeothermy established, etc.). They grow into adults with relatively large brains. [Examples: primates, ungulates, and cetaceans.]

Altricial mammals are usually born in some kind of nest, whereas nests are quite rare among precocial mammals, and postnatal growth in the relatively sheltered conditions of the nest permits altricial mammals to "catch up" to some extent with precocial mammals despite the relatively poor initial state of development of altricial offspring at birth. Nevertheless, there is obviously some limit to this "catching up" process, since precocial mammals typically have larger brains than altricial mammals when they reach adulthood. When clearly precocial mammals ($N = 159$) and clearly altricial mammals ($N = 87$) are analyzed separately, fitting of lines of fixed slopes 0.75 to logarithmically transformed brain and body size data yields the following two equations (E_A = adult brain weight):

1. PRECOICIAL MAMMALS: $\log_{10}E_A = 0.75 \cdot \log_{10}P + 1.90$ (6)

2. ALTRICIAL MAMMALS: $\log_{10}E_A = 0.75 \cdot \log_{10}P + 1.74$ (7)

(A fixed slope of 0.75 is used to facilitate direct comparison.) What this means in practical terms is that precocial mammals grow up into adults which typically have brains some 45 percent bigger than adults of altricial species. This difference is, however, far less than the difference in typical neonatal brain weights between precocial and altricial mammals, as is shown by the following allometric formulae for the empirical relationships between neonatal brain weight (E_N) and maternal body weight (P_M):

1. PRECOICIAL MAMMALS ($N = 72$):

$$\log_{10}E_N = 0.70 \cdot \log_{10}P_M + 1.65 \quad (8)$$

2. ALTRICIAL MAMMALS ($N = 24$):

$$\log_{10}E_N = 0.74 \cdot \log_{10}P_M + 0.88 \quad (9)$$

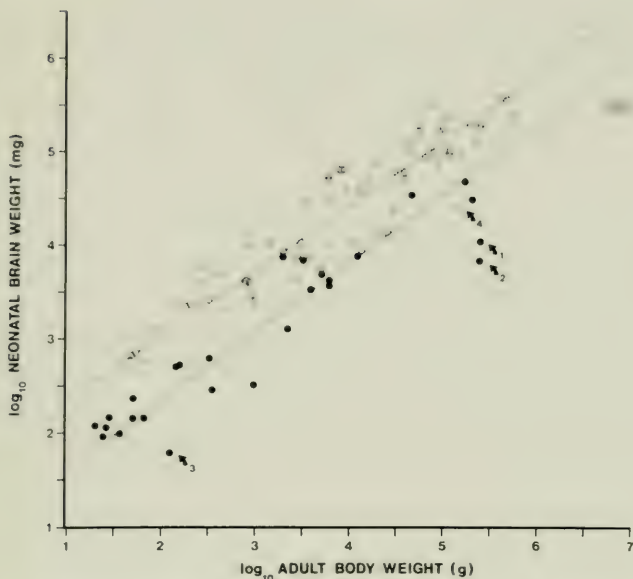


FIG. 6. Logarithmic plot of neonatal brain weight (E_N , in mg) against adult body weight (P , in g) for altricial mammals (black circles; $N = 27$) and precocial mammals (open circles; $N = 72$). Best-fit lines are major axes excluding the following aberrant species (outliers arrowed in figure):

- 1: *Thalarctos maritimus* (lethargic during pregnancy)
- 2: *Ursus arctos* (hibernating during pregnancy)
- 3: *Mesocricetus auratus*
- 4: *Sus scrofa* (unusually large litters)

[Data from Rudder, 1979, and Sacher and Staffeldt, 1974.]

These formulae indicate that precocial mammals have a considerable advantage at birth in terms of neonatal brain weight, which is typically some 4.5 times greater than in altricial mammals (fig. 6).

The distinction between precocial and altricial mammals is important in testing one of the predictions derived from the hypothesis that maternal metabolic turnover (M_M) constrains neonatal brain size (E_N) and hence adult brain size (E_A). For these relationships to lead to a coincidence between the allometric exponents for maternal metabolic turnover and adult brain size (both = 0.75), it must follow that adult brain size scales isometrically ($\alpha = 1$) with respect to neo-

natal brain size. In other words, the relationships should be covered by the following set of formulae (Martin, 1981):

$$\begin{aligned} M_M &= k \cdot P_M^{0.75} \text{ [Kleiber's Law]} \\ E_N &= k' \cdot M_M \\ E_A &= k'' \cdot E_N \\ \text{from which } E_A &= k''' \cdot P_M^{0.75} \text{ [see equation (4)]} \end{aligned} \quad (10)$$

But equation (10) can only be tested realistically if precocial and altricial mammals are examined separately, since the relationships between E_A and E_N are so radically different between these two groups, primarily because of differences in gestation period not allowed for in the above equations. When adult brain weight is plotted against neonatal brain weight for precocial and altricial mammals separately, the following relationships are found (Martin, 1981):

1. PRECOICIAL MAMMALS ($N = 71$):

$$\log_{10} E_A = 0.99 \cdot \log_{10} E_N + 0.42 \quad (11)$$

2. ALTRICIAL MAMMALS ($N = 24$):

$$\log_{10} E_A = 1.01 \cdot \log_{10} E_N + 0.85 \quad (12)$$

In both equations, the value determined for the allometric exponent is very close to unity, so the relationships are indeed virtually isometric (viz., $\alpha = 1$) as predicted. In precocial mammals, adult brain size is typically 2.5 times as big as neonatal brain size, whereas in altricial mammals it is typically 7.5 times as big. Unfortunately, neonatal brain weights have only been recorded for relatively few mammals as yet (Sacher and Staffeldt, 1974; Rudder, 1979), so much remains to be done in investigating this key parameter. The best sample as yet available has been obtained for the order Primates ($N = 27$) and for this particular group of mammals the overall relationship is exactly isometric, with a very high correlation coefficient ($r = 0.992$):

$$\log_{10} E_A = 1.00 \cdot \log_{10} E_N + 0.37 \quad (13)$$

This equation indicates that in primates the size of the adult brain is typically 2.3 times as big as the neonatal brain, though there is a limited range of variation among primate species, with the adult brain reaching between 1.5 and 3.5 times its neonatal size (fig. 7).

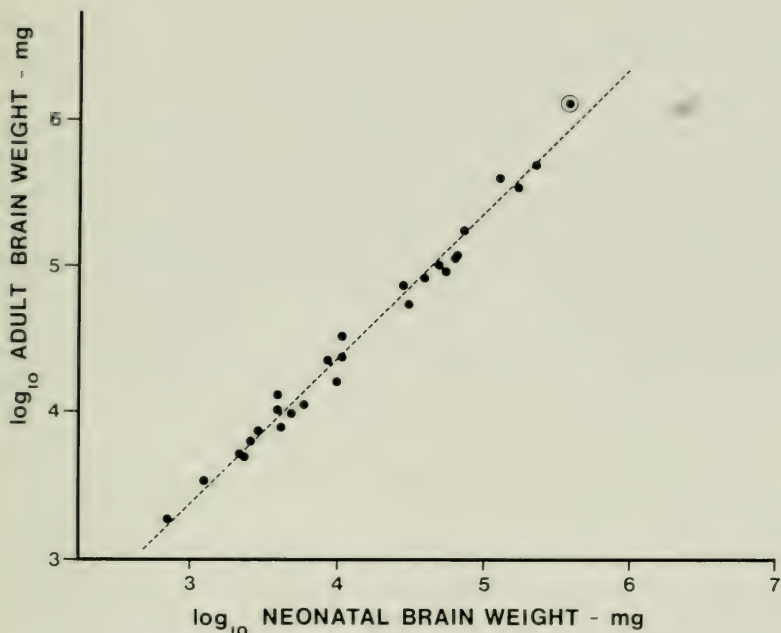


FIG. 7. Logarithmic plot of adult brain weight (E_A , in mg) against neonatal brain weight (E_N , in mg) from primates including man ($N = 27$ species; outlined circle = *Homo sapiens*); data from Rudder (1979). The slope of the best-fit line (major axis) is exactly unity, indicating isometric scaling (viz., simple proportional size increase) of adult brain relative to neonatal brain. There is a small amount of scatter around the best-fit line, reflecting differential adaptation of individual species (see fig. 15), but the point for *Homo sapiens* shows the greatest upward displacement relative to the line.

In fact, the greatest degree of postnatal brain growth is found in *Homo sapiens* with a value close to 3.5 (see later). This limited amount of variation indicates that, although the relationship between adult brain size and neonatal brain size is isometric in primates overall, there is some permissible individual variation between primate species in the partitioning of brain growth between foetal and postnatal stages. That is to say, individual primate species may follow somewhat different strategies within the general constraint of simple proportional (isometric) increase in size of the brain after birth.

It is fairly obvious that a mammal mother's metabolic capacity

must be related in some way to the growth of her foetus over a given gestation period, and one might therefore expect some relationship to exist between gestation period and the size of the neonate and its component organs. Sacher and Staffeldt have examined this question in a seminal paper published in 1974. They found that a much closer relationship existed between gestation period and neonatal brain size than between gestation period and overall neonatal body size. This provides fairly clear evidence of a particularly intimate connection between gestational processes (including the mother's metabolic capacity) and foetal brain growth, thus singling out the brain as an organ of special significance in the maternal-foetal relationship.

BRAIN GROWTH DURING FOETAL AND POSTNATAL LIFE

There is a particularly interesting relationship between the brain size of mammal species during foetal life, which has been independently recorded by Holt and coworkers (Holt et al., 1975; Holt, Renfrew, and Cheek, 1981) and by Sacher (1982) (see also Gould, 1977). When brain weight is plotted against body weight for mammalian foetal stages of any age, using logarithmic coordinates, it is found that primates are clearly separated from all non-primate mammals (fig. 8). In other words, the growth of the primate foetal brain is found to follow a quite different relationship to total foetal body weight when compared with non-primate mammals generally, though odontocete cetaceans (dolphins, etc.) are a special, intermediate case. Best-fit lines for the available data (fig. 8) yield the following formulae for the relationships between foetal brain weight (E_F) and foetal body weight (P_F):

1. PRIMATES ($r = 0.99$): $\log_{10}E_F = 0.95 \cdot \log_{10}P_F + 2.25$ (14)

2. NON-PRIMATES ($r = 0.98$): $\log_{10}E_F = 0.82 \cdot \log_{10}P_F + 1.87$ (15)
(excluding cetaceans)

Although the empirically determined values for the slopes are somewhat different (that for primates being almost isometric), thus hindering a direct comparison between the two groups, it can be stated as a crude approximation that a primate foetus of a given weight

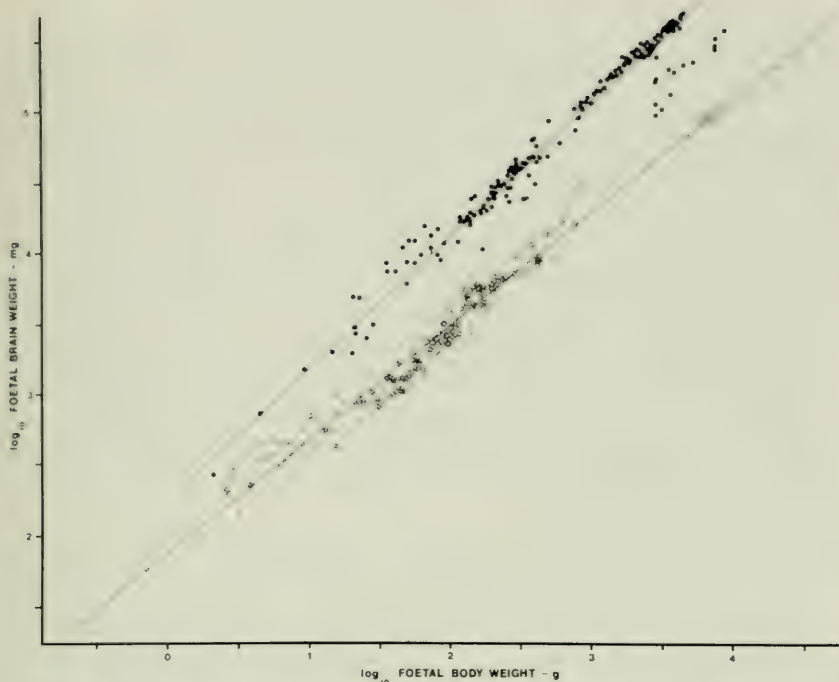


FIG. 8. Logarithmic plot of foetal brain weight (E_F) against foetal body weight (P_F) for primates (black circles), toothed cetaceans (black squares) and other non-primates (open circles). The best-fit lines (major axes) show a major distinction between primates and non-primates. Note that the best-fit line for *Homo sapiens* (uppermost, thin dotted line) coincides very closely with the general best-fit line for primates. Each point represents a single foetus. Data derived from: Latimer (1938), Count (1947), Corder and Latimer (1949), Dickerson and Dobbing (1967), Larroche (1967), Dobbing and Sands (1970), Hendrickx and Houston (1971), Harel et al. (1972), Pirlot and Bernier (1974), Roberts (1975), Holt et al. (1975), Hubert, Stahlheim and Booth (1975), Pirlot and Kamiya (1975), Chambers (1982). These sources yielded 185 points for six primate species (including man) and 305 points for 10 non-primate species.

will typically have a brain weight twice as large as that of a foetus of the same body weight from any other mammal species (see also Sacher, 1982). As yet, data on brain and body weights of foetal stages are only available for a limited number of mammal species and non-primates are particularly poorly represented (fig. 8). For this reason, the distinction between primates and non-primates noted above requires further confirmation. In particular, the data represented in

figure 8 do not include any strepsirhine primate species and numerous non-primate mammal groups are totally unrepresented. But there is some confirmation available for the distinction between primates and non-primates, since the different trajectories shown in figure 8 must logically lead to a difference in the relationship between *neonatal* brain weight and *neonatal* body weight. Sacher (1982) has shown, through an analysis of data from 13 different orders of mammals (see Sacher and Staffeldt, 1974), that there is indeed the expected distinction between all primates (including strepsirhine species) and non-primates in neonatal brain : body weight relationships, with the exception that neonate odontocete cetaceans are again intermediate. The relationships between neonatal brain weight and neonatal body weight for primates and non-primates (fig. 9) are virtually identical with those for foetal development (fig. 8), as predicted:

$$1. \text{ PRIMATES } (r = 0.99): \quad \log_{10} E_N = 0.96 \cdot \log_{10} P_N + 2.12 \quad (16)$$

$$2. \text{ NON-PRIMATES } (r = 0.99): \log_{10} E_N = 0.86 \cdot \log_{10} P_N + 1.85 \quad (17)$$

As Sacher (1982, p. 104) points out, the overall pattern suggests that an "extraordinary evolutionary event took place" in the origin of modern primates: "The schedule of primate fetal development was modified by reducing by half the amount of non-neural somatic tissue associated with a given amount of neural tissue throughout the greater part of fetal life."

Apparently, a similar, but less spectacular, change also occurred in the origin of the odontocete cetaceans.

It must be emphasized that figure 8 conveys no information about *rates* of foetal development and that this omission can be a source of confusion. For example, it might be concluded from the difference between primates and non-primates that foetal brain growth has been relatively accelerated in primates. In fact, it is well known that primates have very slow rates of foetal somatic growth compared to other mammals (e.g., see Payne and Wheeler, 1968), so the distinctiveness of primates is doubtless due to a relative deceleration of foetal body growth rather than to acceleration of foetal brain growth (Holt, Renfrew, and Cheek, 1981; Sacher, 1982). Again, this is just what would be expected from the existence of a more intimate connection between maternal metabolic turnover and foetal brain

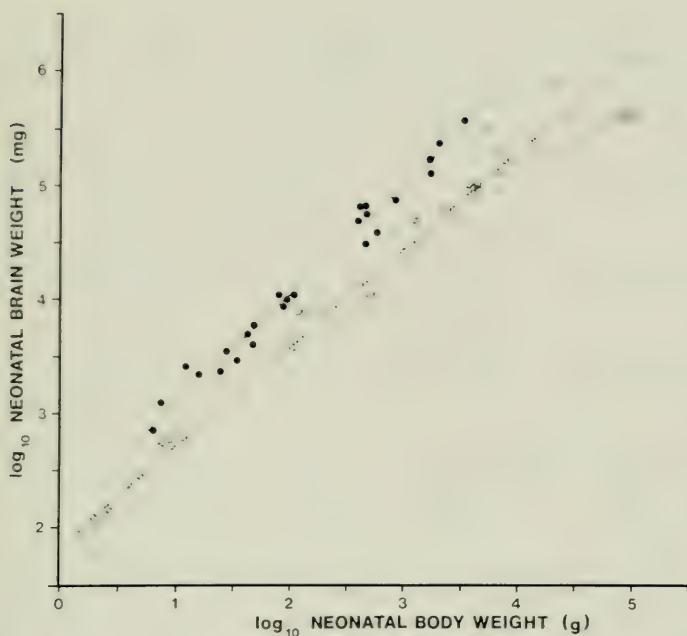


FIG. 9. Logarithmic plot of neonatal brain weight (E_N , in mg) against neonatal body weight (P_N , in g) for primates (black circles; $N = 27$) and non-primates (open circles; $N = 72$). Best-fit lines (major axes) are clearly distinct; toothed cetaceans (open squares; $N = 3$) are again intermediate.

growth than between maternal metabolism and overall foetal body growth. It should also be noted that different primate species may move along the brain growth trajectory shown in figure 8 at different velocities. This is particularly noteworthy in the case of *Homo sapiens*. For instance, the great apes are relatively similar to man in terms of both adult body size (30–100 kg, compared to 57 kg) and gestation period (245–270 days, compared to 270 days; taken from the time of conception in all cases), yet they all produce neonates with brain and body weights approximately half of the neonatal weights found with *Homo sapiens* (table 1). From this it can be concluded that human mothers devote a relatively greater quantity of energy and other resources to foetal brain and body development over a standard time than do our closest relatives among the primates, the great apes. But this is achieved by following at a faster

TABLE 1
Neonatal Brain and Body Weights for Man and the Great Apes

Species	Neonatal Body Weight (g)	Neonatal Brain Weight (g)	Source
<i>Homo sapiens</i>	3375 ¹ (N = 22,413)	384 ² (N = 183)	1. Gibson & McKeown, 1952 2. Jordaen, 1976b
<i>Pan troglodytes</i>	1756 ³ (N = 29)	128 ⁴ (N = 2)	3. Keeling & Riddle, 1975 4. Schultz, 1941
<i>Gorilla gorilla</i>	2110 ⁵ (N = 9)	227 ⁶ (N = ?)	5. Joines, 1977; Nadler, 1974; 6. Schultz, 1965
<i>Pongo pygmaeus</i>	1728 ^{7,8} (N = 14)	170 ⁸ (N = 3)	7. Groves, 1971 8. Rudder, 1979

rate the typical primate brain : body growth trajectory shown in figure 8, without significantly departing from it.

Postnatal growth of the brain is also of particular interest with respect to comparison between man and other primates. As has been pointed out by Holt, Renfrew, and Cheek (1981), growth of the brain from conception onward in mammals can be resolved into two relatively distinct phases, an early period of rapid brain growth relative to body size and a subsequent period of slower brain growth. In mammals with precocial young, such as typical primates, the transition from rapid to slow growth of the brain closely coincides with the time of birth, as can be seen from a graph of brain size against age. With altricial mammals, on the other hand, the rapid growth of the brain characteristic of foetal stages in both altricial and precocial mammals is continued for a short period after birth before there is a point of inflection in the growth curve, followed by slower postnatal brain growth (hence the partial "catching up" by altricial mammals noted above).

It is important at this point to recognize that there are two quite different ways of presenting brain growth data. Traditional graphs of brain growth, following the pattern set for body growth, show

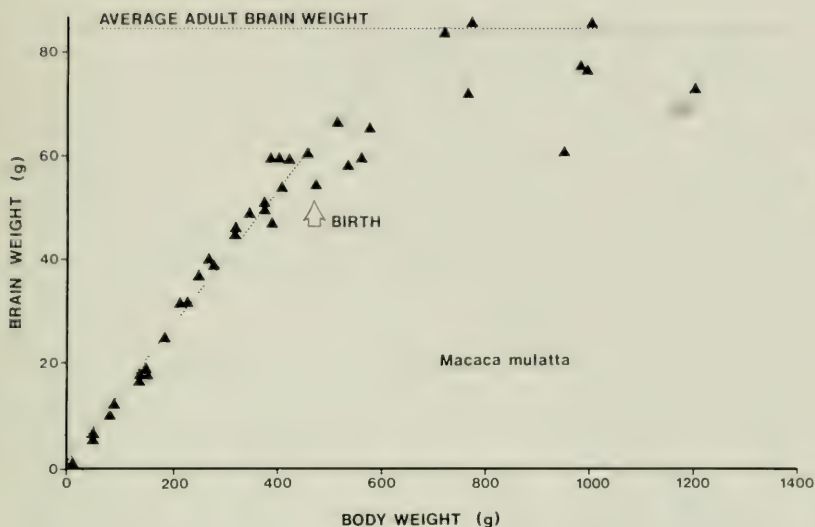


FIG. 10. Plot of brain weight (g) against body weight (g) for developing *Macaca mulatta*. Since the relationship between foetal brain and body weight is virtually isometric [see equation (14)], logarithms have not been used and the major axis (oblique dotted line) has been calculated for the raw data. There is a clear departure from the foetal trajectory at the time of birth in this species, with the brain subsequently developing more slowly with respect to body weight. Data from Holt et al. (1975) and Kerr et al. (1974).

brain size plotted against time and comparisons between species are somewhat complicated. But if brain weight is plotted against body weight on logarithmic coordinates to reflect the trajectory of individual growth, as in figure 8, an approximately straight-line relationship is found for all mammals, though primates and non-primates differ (as shown) in the specific parameters involved. When birth takes place in typical precocial mammals (e.g., primates), further development of the brain follows a flatter trajectory along a line lying beneath the foetal line (as in *Macaca mulatta*—fig. 10). With typical altricial mammals, a similar transition to a flatter trajectory is found, but (as indicated above) this transition is postponed for some time (a period of days or weeks) after birth. *Homo sapiens* is a marked exception to the rule among primates, however, in that the foetal growth relationship between brain and body weight con-

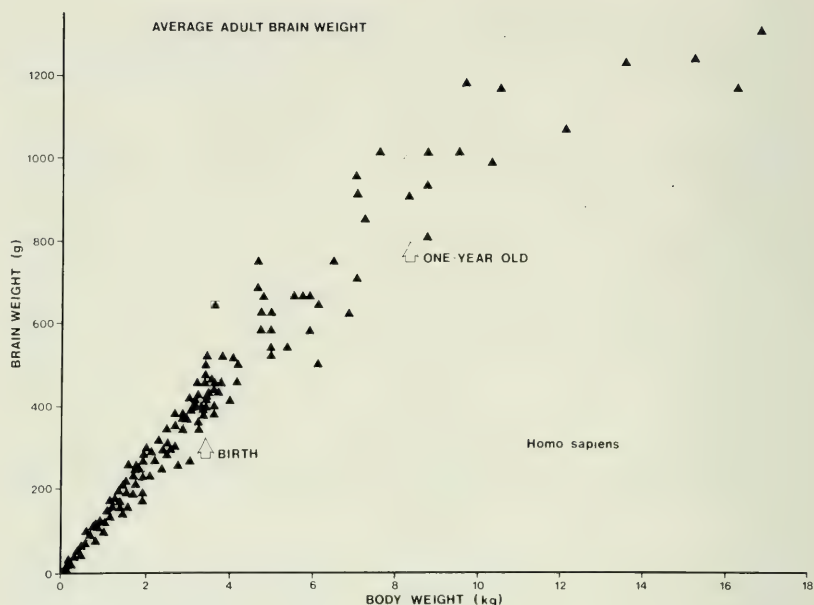


FIG. 11. Plot of brain weight (g) against body weight (kg) for developing *Homo sapiens*. Conventions as for figure 10. Note that there is no clear departure from the foetal trajectory indicated by the major axis (oblique dotted line) until the human infant has reached a postnatal age of approximately 12 months, though scatter about the foetal line increases following birth. Data selected from Larroche (1967), Blinkov and Glezer (1968), Dobbing and Sands (1973), Burn, Birkbeck, and Roberts (1975).

tinues for some time after birth (fig. 11). This peculiarity is connected with the distinctive nature of the human neonate. Although the newborn human infant can correctly be described as precocial in terms of the criteria set out already (see also fig. 5), its degree of helplessness in motor terms is more akin to that found with altricial neonates. It is for this reason that Portmann (1941) referred to the human neonate as "secondarily altricial" and proposed that the one-year-old human infant is closer to the newborn great ape in motor terms (see also Gould, 1977). Portmann cited a number of lines of evidence suggesting that the transition to typical postnatal growth characteristics occurs after the age of one year in humans and concluded that an essentially embryonic growth pattern continues for approximately 12 months after birth. He therefore proposed that

Homo sapiens has the equivalent of a 21-month gestation period, divided into two phases: intrauterine (nine months) and extrauterine (12 months). The plot of brain size against body size for human development (fig. 11) provides dramatic confirmation of Portmann's interpretation, since it clearly shows that a foetal pattern for brain : body relationships is maintained in human ontogeny until at least 12 months after birth. On the one hand, this accounts for the helplessness of young human infants compared with their primate counterparts, since foetal brain growth postponed to the postnatal period may well require relative immobility. On the other hand, the continuation of a foetal pattern of brain growth for such a long period after birth represents a unique feature of *Homo sapiens* in comparison to all other mammals. It is possible, as suggested by Gould (1977), that this special feature of human development can be correctly described as "neotenuous" (i.e., involves the retention of characteristics from earlier growth stages), but the situation is complicated since in other respects human development from conception to 12 months after birth is actually accelerated in comparison with, say, the great apes (see also Leutenegger, 1982).

ECOLOGICAL CORRELATES OF RELATIVE BRAIN SIZE

In recent years, a number of attempts have been made to relate relative brain size in primates and other mammals to ecological parameters, notably with respect to feeding ecology (e.g., Eisenberg and Wilson, 1978; Clutton-Brock and Harvey, 1980; Harvey, Clutton-Brock, and Mace, 1980; Mace, Harvey, and Clutton-Brock, 1980, 1981; Mace and Eisenberg, 1982). Among the primates, a particularly good example is provided by analysis of relative brain size in Old World monkeys and apes (Cercopithecoidea + Hominoidea) in relation to differential adaptation for predominant frugivory or predominant folivory. It has been shown by Clutton-Brock and Harvey (1980) that in several primate groups the more frugivorous species tend to have larger brains than related species which can be regarded as specialized folivores. Following the procedure advocated by these authors, one can take generic average values for \log_{10} brain weight

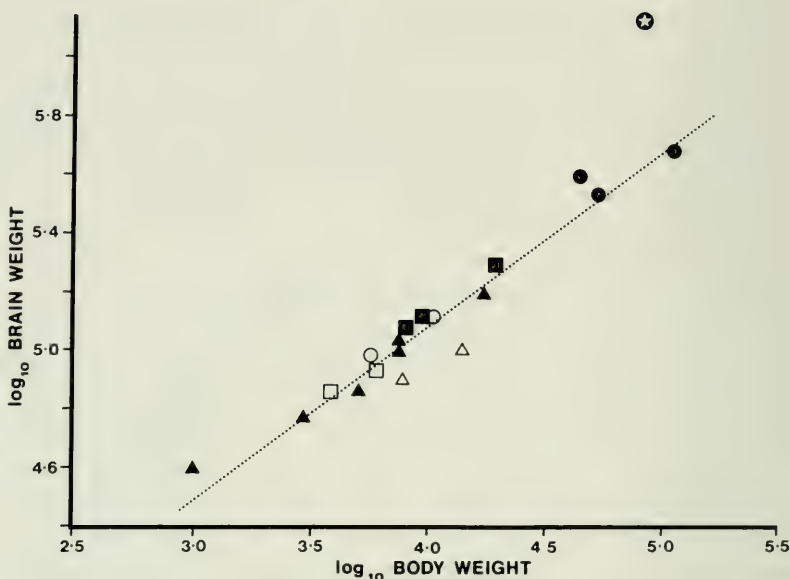


FIG. 12. Plot of average logarithmic values for adult brain weight (E_A , in mg) against adult body weight (P_A , in g) for individual genera of Old World monkeys and apes (Cercopithecoidea + Hominoidea). The best-fit line (major axis) was determined for all genera excluding *Homo*.

Key: Black triangles = forest-living cercopithecines (most *Cercopithecus*; *Miopithecus*; *Allenopithecus*; *Cercocebus*; *Cynopithecus*; *Mandrillus*); open triangles = colobines (*Colobus*; *Presbytis*); open squares = transitional (forest/open-country) cercopithecines (*Cercopithecus aethiops*; *Macaca*); black squares = open-country cercopithecines (*Erythrocebus*; *Papio*; *Theropithecus*); open circles = lesser apes (*Hylobates*; *Symphalangus*); black circles = great apes (*Gorilla*; *Pan*; *Pongo*); white star in black circle = *Homo sapiens*.

[N.B. *Cercopithecus aethiops* has been treated separately from other *Cercopithecus* species because of its distinctive ecological features.]

and \log_{10} body weight (to avoid bias by species-rich genera) and obtain a best-fit line for the data (fig. 12). Following the general rule, this line has a lower slope value than that for the primates as a whole, but it can be taken as the appropriate line for comparison among the Old World monkeys and apes:

$$\log_{10} E = 0.60 \cdot \log_{10} P + 2.68 \quad [r = 0.97] \quad (18)$$

It is clear from figure 12 that two genera other than *Homo* lie well

above the best-fit line (*Miopithecus*; *Pan*), whereas the two colobine monkey genera included (*Colobus*; *Presbytis*) lie well below the line. Taking the best-fit line (major axis) as a reference standard, it is possible to calculate special encephalization quotient values (EQ_{OW} = Old World simian encephalization quotient) for the individual species for which data are available. These values are plotted in histogram form in figure 13, which shows that there is no overlap between colobine (leaf-monkey) species and the cercopithecine monkeys + apes. The colobines, which have specialized sacculated stomachs for processing leaf material, all have EQ_{OW} values of less than 0.8. Among the cercopithecine monkeys, it can be seen that there is no obvious distinction between forest-living and savanna-living species (e.g., indicating larger brains in the latter). Indeed, the largest EQ_{OW} value (1.38) is found in the forest-living *Miopithecus talapoin*, so a shift to savanna alone does not correlate with increased brain size. In line with this, the forest-living hylobatids (lesser apes: gibbons and siamang) fall within the cercopithecine monkey range. Finally, the chimpanzee (*Pan*) has a very large EQ_{OW} value of 1.35, whereas the orang (*Pongo*) and the gorilla (*Gorilla*) have only moderate values (1.05 and 0.95, respectively). Among the great apes, the sequence in relative brain size (*Pan* > *Pongo* > *Gorilla*) matches a dietary spectrum ranging from predominant frugivory to predominant folivory, once again confirming the correlation between diet and brain size.

Given these facts, it is possible to frame an explanatory hypothesis in terms of the differential central nervous processing capacity which might be required for feeding on relatively scarce fruiting trees, which tend to be very clumped in both space and time. Feeding upon leaves, which may be regarded as being both more abundantly available and more evenly distributed, might be thought to be less demanding in terms of central nervous processing. This type of explanation has been explicitly proposed by Clutton-Brock and Harvey (1980) and by Mace, Harvey, and Clutton-Brock (1980).

A similar correlation between relative brain size and dietary habits has been found among the bats (Pirlot and Stephan, 1970; Eisenberg and Wilson, 1978; Stephan, Nelson, and Frahm, 1981). Overall, it has now been clearly demonstrated that fruit-eating bats have con-

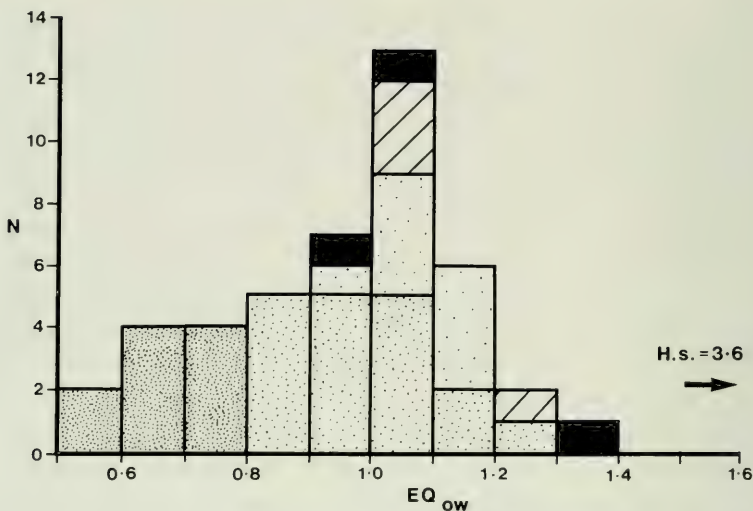


FIG. 13. Histogram of encephalization quotient values (EQ_{ow}) calculated for individual Old World monkey and ape species in relation to the best-fit line shown in figure 12.

Key: Heavy stippling = colobines; medium stippling = forest-living cercopithecines; light stippling = open-country cercopithecines; hatching = lesser apes; black = great apes.

Note that the colobines uniformly have the lowest values (EQ_{ow} less than 0.8) and that there is no overall distinction between forest-living monkeys and lesser apes and open-country monkeys.

siderably larger brains than insect-eating bats, by a factor of approximately two, and that bats with other feeding habits (e.g., nectar-feeding or fish-eating) have intermediate brain sizes. Once again, it has been explicitly proposed that fruit-eating bats require larger brains than other bats, notably the insectivorous forms, because fruits occur as scattered resources which demand an enhanced central nervous processing capacity for their exploitation. Insectivorous bats, it is argued (Eisenberg and Wilson, 1978) do not require such large brains to locate their insect prey.

Now, while it may seem likely that location of scattered food sources, such as fruits, may require more central nervous processing than foraging for relatively abundant food items, such as leaves, it is by no means obvious that hunting for insects (as in the use of

echolocation in microchiropteran bats) is comparatively undemanding in central nervous terms. Further, since it is now widely recognized that the presence of secondary compounds in many leaf species may require considerably greater selectivity in leaf-eating than might be expected at first sight (Freeland and Janzen, 1974; McNab, 1978), it seems likely that folivores may well exhibit quite complex feeding strategies in comparison to frugivores. Once again, we have a situation where a correlation between two variables (relative brain size; foraging behavior) has been interpreted as a *causal relationship* assumed to operate in a given direction. There is, in fact, an alternative explanation which can be advanced in terms of the energy cost of brain development. McNab (1980) has shown that fruit-eating bats have higher metabolic rates than insect-eating bats, once scaling to body size is taken into account. Fruit-eating bats have metabolic rates closely agreeing with the values expected for mammals generally from Kleiber's standard equation (1961), whereas insectivorous bats have values some 50 percent lower than expected. As with relative brain size, bats with other forms of feeding behavior are intermediate in terms of basal metabolic rate. Therefore, it can be suggested that insectivorous bats have smaller relative brain sizes than frugivorous bats because of their lower metabolic turnover. More precisely, it can be proposed that low metabolic rates in gestating female insectivorous bats constrain foetal brain growth such that neonatal brain size is limited in comparison to frugivorous bats. Given general isometric scaling of adult brain size with respect to neonatal brain size, it should automatically follow that adult frugivorous bats would end up with larger brains than adult insectivorous bats. Indeed, since maternal metabolic turnover must obviously constrain foetal development, the difference in basal metabolic rate between frugivorous and insectivorous bats should *inevitably* lead to a difference in adult brain size between these two groups unless there is some systematic difference (e.g., in gestation period) to offset the limitation imposed by low metabolic rate in insectivorous bats.

Unfortunately, data are not yet available for basal metabolic rate in colobine monkeys, so it is not possible to test the prediction that these monkeys, like insectivorous bats, have relatively low metabolic

rates. Nevertheless, McNab (1978, 1980) has shown that in mammalian folivores generally there is a lowering of basal metabolic rate relative to Kleiber's equation for mammals, and this effect increases as the proportion of leaves in the diet increases. It therefore seems highly likely that colobines will be found to have low metabolic rates in comparison with other Old World simians, and this would explain why they have relatively small brains independently of any hypothesis based on the central nervous processing capacity required by their predominantly leaf-eating foraging strategy.

As yet, it is not possible to decide which of the two competing hypotheses (requirements of foraging behavior; limitation imposed by maternal metabolic turnover) best explains differences in relative brain size between mammal groups with different dietary habits. However, there is increasing evidence to show that specialization on leaves or on insect food entails a metabolic cost because of toxic compounds present in the food items which have been developed to discourage predation. It follows from this that specialized mammalian folivores and insectivores will commonly have low metabolic rates as a mechanism for reducing total food intake and hence the burden of ingested toxins (McNab, 1978, 1980). Thus, specialized folivores and insectivores must be expected to have relatively small brains on straightforward metabolic grounds unless they have developed special adaptations (e.g., extension of the gestation period) to offset the limitation imposed by low maternal metabolic turnover during foetal development.

Thus far, gestation period has been taken into account only in a very broad sense through the distinction between precocial mammals (relatively long gestation periods) and altricial mammals (relatively short gestation periods); but it is possible for this parameter to be modified in individual species with corresponding consequences for brain development. In fact, gestation period is just one of the parameters that combine to determine the level of maternal investment in offspring in any mammalian species. In recent years, it has become increasingly clear that differential reproductive strategies in mammals, including differential levels of maternal investment, can be interpreted with respect to the spectrum from r-selection to K-selection (MacArthur and Wilson, 1967; Pianka, 1970),

thus placing maternal investment firmly in a broad ecological context. In relatively unstable habitats or in habitats with extreme seasonal changes many animal species are subject to drastic mortality, and the theoretical carrying capacity (K) of the environment is rarely attained. Under such conditions, resources are usually not limiting and natural selection will tend to favor maximization of the intrinsic rate of natural increase (r_{\max}) and rates of development (r -selection). In relatively stable habitats, by contrast, many animal species will exist for much of the time at or near carrying capacity and natural selection will favor increased efficiency of utilization of environmental resources, including limitation of reproductive turnover (K -selection). It is characteristic of K -selecting environments that competition, both within and between species, is intense, and the relatively few offspring that are produced are typically provided with enhanced parental investment of some kind. There is obviously a close correspondence between the r -selection/ K -selection distinction and the altricial/precocial neonate difference among mammals, in that the reproductive features of altricial mammals (e.g., large litter-size) are related to high reproductive turnover, whereas those of precocial mammals (e.g., relatively long gestation period) are indicative of increased parental investment in individual offspring. The primates, with their precocial offspring, fit the K -selection category very well, as might be expected from the fact that they have typically been inhabitants of tropical and subtropical forests for the last 50 million years at least. Correspondingly, primates have relatively long gestation periods compared with other mammals and this relative extension is found in other key parameters of the life-cycle, such as age of attainment of sexual maturity and maximum lifespan. But with the order Primates there is also scope for special adaptation of reproductive strategies in individual species. The lorises (lorises, potto, angwantibo), for example, are characterized by low basal metabolic rates and sluggish locomotion to match, yet the adults end up with relative brain sizes comparable to those of their fast-moving relatives, the galagines (bushbabies), because the gestation period is relatively longer in lorises and allows for more foetal brain growth, thus offsetting the limiting effect of the mother's low metabolic turnover. Such particular adaptations of individual species are common,

as is apparent from analysis of the differential partitioning of brain growth between foetal and postnatal life (see later) and it is here that one might seek special adjustments for specific behavioral requirements. Although primates as a group appear to be K-selected compared with certain other mammals (e.g., most rodents and insectivores), some degree of variation is to be expected since some primate species inhabit relatively K-selecting tropical rainforest while others occur in drier, more open environments which are likely to exert some r-selecting effect. The picture is further confused by the fact that different strategies can be followed within the same environment, but as far as primates are concerned the situation can be simplified into four alternative outcomes in terms of overall energy budgets (fig. 14). In tropical rainforest, which is probably the typical environment to which most primates have been adapted during their evolution, K-selection has generally led to restriction of the proportion of the energy budget available for reproduction, but because of enhanced investment in individual offspring, gestation periods are long and brain size is therefore usually quite large in both neonates and adults. Under K-selecting conditions, competition is fierce and this may well explain why certain forest-living primate species (e.g., lorises, owl-monkeys, and possibly colobines) have developed a strategy of lowering basal metabolic rates. This permits them to feed on certain foods (e.g., some arthropods; leaves) which are protected by toxic substances, though at the cost of reducing overall metabolic turnover. (Maximum metabolic turnover is directly related to basal metabolic rate; McNab, 1980.) Mammals with low basal metabolic rates are sluggish, at least in part because the proportion of body weight devoted to muscle decreases with decreased metabolic turnover (McNab, 1978) and the energy available for reproduction is even more curtailed. Hence, such species can only possess relatively large brains if gestation periods are extended to offset the effect of low maternal metabolic rate on foetal brain growth.

Should a forest-living primate species subsequently become adapted for living in open country, the relative r-selecting effect of this environment may have a number of possible outcomes (fig. 14). In any event, since food availability is not usually a pronounced limiting factor as it is in rainforest, constraints on the overall energy

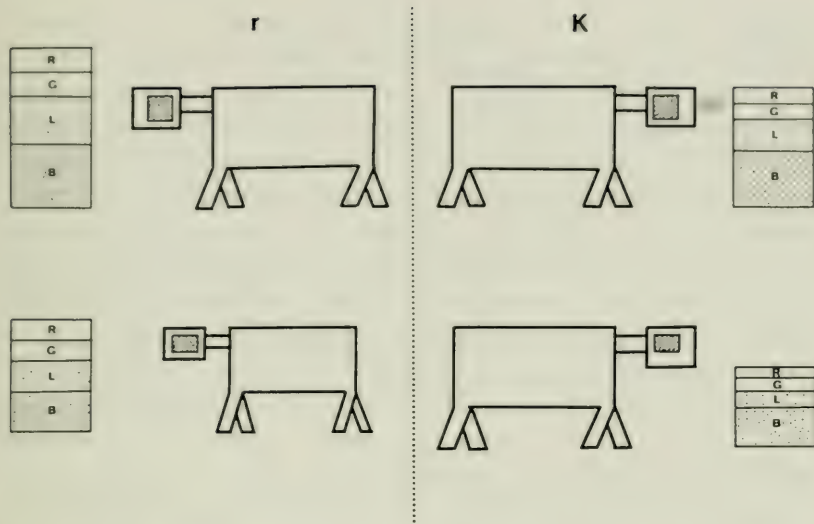


FIG. 14. Schematic illustration of possible effects of K-selection vs. r-selection with respect to overall metabolic turnover and brain size. A relatively K-selected species with a typical mammalian basal metabolic rate (top right) will have a moderate energy budget. A large part of this budget will be represented by basal metabolism (B), with moderate locomotor expenditure (L) generating through food-acquisition the energy required for maintenance, growth and repair (G) and reproduction (R). Under the intensive competition typical of K-selecting conditions, some species may adopt a "low-energy strategy" (bottom right), involving reduced metabolic rate (B) and limitation of energy available for locomotion (L), growth (G) and reproduction (R). Unless special adaptations are developed (e.g., extension of gestation period), such a low-energy strategy will result in a relative limitation of brain size, as in colobine monkeys. Under r-selecting conditions, a mammal species of the same body size (top left) will typically devote a greater proportion of its energy budget to reproduction (R) and faster growth processes (G). Since basal metabolic rate is unlikely to change, a large brain size can only be maintained if a "high-energy strategy" is adopted, involving greater investment of locomotor energy (L) to permit increased harvesting of food. An alternative outcome under r-selecting conditions is relative reduction of body size which will lead (among other things) to increased reproductive potential. Again, brain size can only remain relatively large if a "high-energy strategy" is adopted.

budget are relaxed to some extent. For this reason, it is unlikely that a strategy of feeding on toxin-rich foods and lowering basal metabolism will develop, and certainly no open-country primate species seems to have adopted such a strategy. On the other hand, open-

country primates must to some extent respond to the pressure exerted by r-selection toward increased reproductive output. In mammals, an increase in reproductive potential can be achieved in various ways, such as by an increase in litter-size (usually accompanied by a reduction in gestation period) or through earlier attainment of sexual maturity, and the latter mechanism seems to be predominant among open-country primates. Hence, primates exposed to r-selecting conditions can increase their energy budgets (in comparison to their forest-living counterparts), but they are also constrained to invest more in reproductive turnover. One of the easiest ways for the latter to be achieved is through reduction in body size, which is also likely to entail a reduction in gestation period and other parameters, though it is theoretically possible for a species to remain the same size after shifting from forest to more open country and for the greater energy budget to allow for increased reproductive output without requiring any reduction in parameters such as brain size. Hence, a primate species living under open-country conditions can have the same brain and body size as a forest-living counterpart, though it will theoretically have a higher overall metabolic throughput and a higher reproductive potential. It is clear from figure 13 that open-country cercopithecines do not tend to have larger brains than their forest-living counterparts and fully overlap with them. As noted above, the largest relative brain size is found in the forest-living talapoin among the cercopithecine monkeys.

These considerations present certain problems for the prevailing theory of human evolution, according to which the definitive changes are related to a shift from forest to open-country conditions (the so-called "savanna theory"). In terms of general ecological pressures, such a shift would not have favored development of the particular human combination of a very large brain size with extremely slow reproductive turnover. For, when body size is taken into account, it is found that all the critical parameters of the human reproductive life-cycle (age of attainment of sexual maturity; gestation period; longevity) are greater than in any other primate species (or, indeed, any other mammal species). In other words, the combination of large brain size and slow reproductive turnover in *Homo sapiens* is indicative of the operation of an extreme form of K-selection, not

of exposure to r-selecting conditions. It could, of course, be argued *post hoc* that human cultural attributes permit our species to create relative stability in environments which to other species are unpredictable, but it is difficult to understand how *gradual* increase in human brain size (see later), and hence gradual increase in the overall intellectual capacity required for cultural developments, could have taken place under relatively r-selecting conditions out in the savanna. Whereas relative brain size may well be maintained in K-selected species which move from forest to open country, as seems to have been the case with savanna-living cercopithecine monkey species, it is difficult to see how r-selecting environmental conditions could favor any further increase in brain size (see also Rudder, 1979).

THE SPECIAL FEATURES OF HUMAN BRAIN EVOLUTION

The foregoing comparisons have demonstrated that *Homo sapiens* shares a number of general features of brain size and its development with the other primates, most notably in producing precocial offspring and in the shift to a distinctive relationship between brain size and body size during foetal development (fig. 8). But human beings also exhibit a number of special features which set them apart from other primates, or at least from their closest relatives the great apes. These may be listed as follows:

- (i) The remarkably large size of the adult brain relative to body size.
- (ii) The rapid development of both brain and body during foetal development, resulting in a distinctively large brain and body size at birth, compared to great apes.
- (iii) The greater degree of postnatal growth of the brain, accomplished by continuation of foetal brain : body relationships for at least one year after birth and associated with the "secondary altricial condition."

The distinctiveness of *Homo sapiens* with respect to the last two features is somewhat obscured because of variation between primate species in the partitioning of brain growth between foetal and post-

natal stages. For instance, the degree of postnatal brain growth in humans is greater than in any other primate species, but there is considerable scatter about the best-fit line in a plot of adult brain size against neonatal brain size (fig. 7). Similarly, there is some variation among primate species in the degree to which the brain develops *in utero*. However, it is to be expected that overall there should be an inverse relationship between the two phenomena, since species which have a relatively large degree of brain development *in utero* are likely to have less postnatal brain growth. This relationship can be further explored by calculating indices for both foetal and postnatal brain growth. The *foetal brain growth index* can be calculated using the empirical allometric formula determined for the relationship between neonatal brain size and adult body weight in primates ($N = 30$):

$$\log_{10} E_N = 0.83 \cdot P_A + 1.46 \quad (r = 0.96) \quad (19)$$

For each species, the "expected" brain size of the neonate can be calculated from the adult body weight using this formula and the ratio of actual to expected neonate brain size provides an index of the amount of foetal brain growth compared to the norm for primates. Since total postnatal growth of the brain is isometric relative to neonatal brain size, the *postnatal brain growth index* can be calculated by simply dividing adult brain size by neonatal brain size. As mentioned above, the average value for the ratio of adult to neonatal brain size is 2.3 in primates (see also fig. 7). These two indices can then be plotted against one another to examine the partitioning between foetal and postnatal growth in primates. When this is done (fig. 15) it emerges that there is indeed a negative relationship between the postnatal brain growth index (PI) and the foetal brain growth index (FI):

$$PI = 3.07 - 0.78 \cdot FI \quad (r = -0.60) \quad (20)$$

In other words, as expected, species which have a relatively high degree of foetal brain development typically have relatively little postnatal brain development and vice versa. When the data are analyzed in this way, it emerges that *Homo sapiens* is quite distinctive in the combination of greater than expected foetal brain

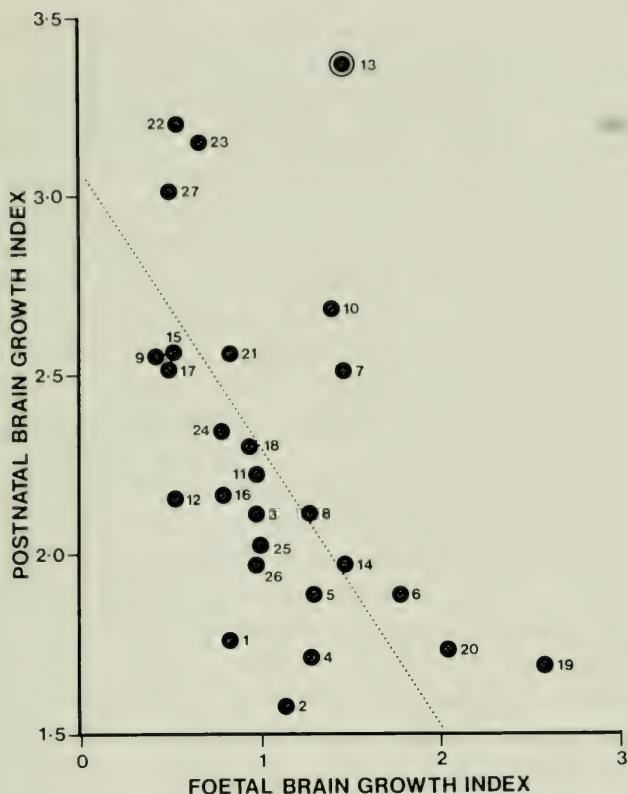


FIG. 15. Plot of postnatal growth index (PI) against foetal growth index (FI) for the brain in 27 primate species. FI is calculated with respect to equation (19) and indicates, for each primate species, the degree to which the brain has developed at birth in comparison to the typical primate condition (FI = 1). PI is simply calculated by dividing adult brain weight by neonatal brain weight to indicate the degree of postnatal brain development (average PI for primates = 2.3). Man has the highest value for PI and one of the highest values for FI; since there is an overall negative correlation between PI and FI (dotted line = major axis excluding *Homo sapiens*), this combination is quite unique.

Key:

- | | | |
|-----------------------------------|---------------------------------|-------------------------------|
| 1. <i>Alouatta palliata</i> | 10. <i>Galago demidovii</i> | 19. <i>Macaca mulatta</i> |
| 2. <i>Aotus trivirgatus</i> | 11. <i>Galago senegalensis</i> | 20. <i>Macaca nemestrina</i> |
| 3. <i>Arctocebus calabarensis</i> | 12. <i>Gorilla gorilla</i> | 21. <i>Microcebus murinus</i> |
| 4. <i>Ateles geoffroyi</i> | 13. <i>Homo sapiens</i> | 22. <i>Nycticebus coucang</i> |
| 5. <i>Callimico goeldii</i> | 14. <i>Hylobates lar</i> | 23. <i>Pan troglodytes</i> |
| 6. <i>Callithrix jacchus</i> | 15. <i>Lemur catta</i> | 24. <i>Papio cynocephalus</i> |
| 7. <i>Cebus capucinus</i> | 16. <i>Lemur fulvus</i> | 25. <i>Pongo pygmaeus</i> |
| 8. <i>Colobus polykomos</i> | 17. <i>Lepilemur mustelinus</i> | 26. <i>Saguinus oedipus</i> |
| 9. <i>Galago crassicaudatus</i> | 18. <i>Loris tardigradus</i> | 27. <i>Varecia variegata</i> |

growth with the maximum observed degree of postnatal brain enlargement. *Homo sapiens*, with a foetal brain growth index value of 1.48, is surpassed only by three primate species among those surveyed: *Callithrix jacchus*, *Macaca nemestrina*, and *Macaca mulatta*; and all of these species exhibit conspicuously low values (1.66–1.88) for the postnatal brain growth index. When the human value for the foetal brain growth index is used to calculate an expected value for PI from equation (20), it emerges that the human brain grows by a factor of 1.8 more than expected for a typical primate species during the postnatal period. This enhancement of postnatal brain growth is doubtless attributable largely or exclusively to the special extension of foetal brain : body relationships through the first year of postnatal life (fig. 11).

As a general rule, it is presumably more efficient in energetic terms for brain growth to take place during foetal life as far as possible, since the mother's metabolic capacity is considerably greater than that of her neonate. Postnatal brain growth requires the developing infant (operating at a high metabolic rate per unit body weight because of its small body size) to convert material supplied in the mother's milk into brain tissue, and this is undoubtedly less efficient. It is therefore striking that so much of human brain growth takes place after birth, but this is because of the constraints of pelvic dimensions in the human female (as was suggested by Portmann, 1941, though he later discarded this interpretation). The human foetus does in fact grow very rapidly compared with that of a great ape, reaching approximately twice the size for both brain and body in a gestation period which is only slightly longer. By that stage, however, the human infant has reached the limit imposed by the mother's pelvis and birth must take place. Hence, the extension of the foetal pattern of postnatal brain growth into the first year of postnatal life in humans represents a special mechanism to circumvent the limitation on neonatal head size imposed by the pelvis. That this is so is confirmed by examination of the relationships in odontocete cetaceans, which have very large relative brain sizes (fig. 3) but only a rudimentary pelvis that is unlikely to limit head size of the neonate at birth. The bottle-nosed dolphin (*Tursiops truncatus*) has an adult body weight of about 155 kg and a gestation

period of about 11 months; it produces a neonate weighing 20 kg with a brain weight of 770 g, which approximately doubles through postnatal growth to reach the adult brain weight of 1600 g (Sacher and Staffeldt, 1974). Reference to equation (11) shows that this is a relatively small amount of postnatal brain growth for a precocial mammal, whereas from equation (8) it can be seen that the neonatal brain size is unexpectedly large (by a factor of about 4) for a precocial mammal. Hence, the evidence is that *Tursiops truncatus* achieves a large adult brain size by enhancement of foetal brain growth, rather than through increased postnatal brain growth, as would be expected in the absence of any maternal pelvic constraint at birth. It therefore seems reasonable to accept the interpretation that pelvic constraints require considerable postnatal development of the brain in *Homo sapiens* (Jordaan, 1976a; Gould, 1977; Leutenegger, 1982).

Continuation of the foetal pattern of brain and body growth into the first year of postnatal life in human beings also poses special problems with respect to lactation, since it is quite clear that a pattern of early postnatal brain growth that is unique among mammals must require a unique milk to supply the needs of the developing human infant. It is, of course, possible that the great degree of postnatal brain development in human beings merely requires the provision of standard nutrients in greater quantities. However, it is also possible that human breast milk contains components which are not normally present in significant quantities in the milk of other precocial mammals with a normal pattern of postnatal brain growth, such as the cow. The widespread use of modified or unmodified cow's milk formulae as a substitute for human breast milk therefore deserves special attention from the point of view of early postnatal brain development. It has been shown that human milk differs from cow's milk in numerous respects (Gaull, 1979; Gaull et al., 1982) and some of the differences may well be specifically relevant to brain development. In particular, human milk differs markedly in its lipid constituents in that long-chain unsaturated fatty acids (especially oleic acid) predominate and there are several differences in amino acid and protein content. The whey protein : casein ratio is inversed in human milk compared to cow's milk and human milk has a considerably greater availability of non-protein nitrogen. In human

milk free amino acids are present in far greater concentrations and in quite different proportions, and the free "amino acid" taurine is particularly noteworthy in that it has been specifically implicated in brain development (Gaull, 1979) and is more than 30 times more concentrated in human than in cow's milk.

In view of these pronounced biochemical differences between human and cow's milk and the special requirements of the developing human brain, it is pertinent to ask whether substitution of cow's milk for human milk leads to deficits in early human brain development. This question does not seem to have been asked very often and it is hence significant that there is some evidence for such deficits (Menkes, 1977; Rodgers, 1978). Rodgers, in particular, took great care to exclude the effects of possible confounding variables (e.g., social class, family size, birth order, etc.) and still detected a significantly greater degree of intellectual impairment in bottle-fed children compared with breast-fed children. This is all the more remarkable in that almost all the children involved (2424 individuals in the 1946 birth cohort included in the U.K. National Survey of Health and Development) were weaned from milk before the age of 12 months (82.2 percent of breast-fed children and 57.5 percent of bottle-fed children in fact received no further milk after 10 months of age). Such early weaning itself presents problems, since typical foetal relationships between the growing brain and body weight persist for at least 12 months after birth in human infants (fig. 11) and there was actually a bias *against* breast-fed infants in the sample, since they were generally weaned earlier. In addition, some of the apparent confounding variables identified in Rodgers's analysis may actually be secondary effects related to breast feeding; for instance, children that were born first in the birth order were also more likely to have been breast fed. Overall, it is clear from Rodgers's analysis that there is *some* link between breast feeding and subsequent intellectual development, though it has not yet been demonstrated that this link is a direct one between milk biochemistry and brain development. Further, it must be remembered that artificial milk formulae have been considerably modified since 1946 (the date of birth of the cohort studied by Rodgers) and that the present-day situation could be rather different. Nevertheless, Ounsted (1982) has reported

significant differences between neurobehavioral test scores of breast-fed versus bottle-fed infants where modern artificial milk formulae were used and, given the peculiar features of early postnatal brain development in human beings outlined above, the relationship between breast feeding and brain maturation obviously deserves more detailed examination.

THE FOSSIL RECORD OF HUMAN BRAIN SIZE

Even a superficial comparison of modern man and the great apes reveals that there are three particular features which involve marked morphological differences in humans: the very large brain, bipedal striding, and dental restructuring. These three features are all clearly connected in that locomotion and food processing underlie the provision of energy for the development and maintenance of a large brain. In terms of the approach adopted here, it can be argued that the uniquely large relative size of the human brain (compared with other primates) requires a relatively high energy flow through the mother, whereas the relatively slow reproductive turnover of modern *Homo sapiens* implies that this strategy required comparative stability in the availability of food resources for its evolution. A further perspective on the evolutionary background to these special human characteristics is provided by the fossil evidence for human evolution (Tobias, 1971) and this permits us, in particular, to ask extremely pertinent questions about the timing and rate of human brain size evolution.

There are now numerous fossil hominid skulls for which cranial capacities have been determined (Tobias, 1971; Holloway, 1973a, 1973b, 1978) and it is possible to interpret these in phylogenetic terms through comparisons with *Homo sapiens* and other primates. Because the great apes are man's closest relatives, it has been traditional to compare hominid fossil cranial capacities particularly with the great apes and modern humans. However, two problems have bedeviled attempts to interpret quantitative data on hominid fossil cranial capacities. In the first place, earlier authors frequently did not take body size and accompanying scaling effects into account,

and this led to an underestimation of the degree of brain development in *Australopithecus africanus*, the earliest well-documented species in hominid evolution. It is generally accepted that *A. africanus* was smaller in body size than any of the modern great apes and man and it is therefore misleading to state, without any proviso, that cranial capacities of gracile australopithecines fall within the range of the modern great apes. The scaling effect of body size on australopithecine brain size has been taken into account only relatively recently (Schaeffer, 1962; Stephan, 1972; Holloway, 1973a; Jerison, 1973; Pilbeam and Gould, 1974) and there are still many authors who continue to imply that the evolutionary expansion of the human brain postdated the australopithecine level and was confined to the last two million years of human evolution (via *Homo habilis* and *Homo erectus* to *Homo sapiens*). Of course, calculations which take into account the effect of body size as a factor in hominid brain evolution depend upon reliable estimates of body weight in fossil hominids, but increasing attention has now been paid to this (Schaeffer, 1962; Stephan, 1972; Kinsey, 1972; Jerison, 1973; McHenry, 1974a, 1974b, 1976; Pilbeam and Gould, 1974; Steudel, 1980; Cronin et al., 1981) and a consensus is slowly emerging. Certainly, we are now moving away from the previous unsatisfactory situation where hominid brain size was considered in relation to geological time with no reference at all to body weight (e.g., see Lestrel and Read, 1973; Lestrel, 1975). Once estimates of body size are taken into account for *Australopithecus africanus*, it emerges that brain size was, at the very least, 30 percent larger than would be expected for a modern great ape of the same body size (see later). But even this is likely to be an underestimate of the evolutionary advancement of the brain in gracile australopithecines because of a second problem which has been given virtually no mention in the literature. Comparison of hominid fossils with modern great apes (and other primates) involves the hidden assumption that relative brain size in modern primates can be equated with the ancestral condition from which great apes and man diverged. Since there has been a general trend toward brain size expansion throughout the mammals (Jerison, 1973; Martin, 1973), such a "living fossil" approach represents no more than a crude approximation to the real

situation. In fact, it is quite likely that there has been some expansion of the brain, relative to body size, in all the lineages which diverged from the common ancestor of the great apes and man (viz., the ancestral hominoid), with the modern forms differing only in the degree to which this has occurred. Hence, if we were able to compare *Australopithecus africanus* with the ancestral hominoid, rather than with modern great apes, its relative brain size would doubtless be found to be even more advanced. Thus, as recognized by Stephan (1972) and by Jerison (1973), evolutionary expansion of the human brain began prior to the earliest known australopithecines in which cranial capacity is measurable. Hence, attempted explanations of human brain size evolution must take into account the fact that brain expansion began prior to known dates for the first appearance of definite stone tools and therefore prior to any hard evidence for subsistence activities (e.g., hunting) dependent upon such implements. Hypotheses which link human brain size expansion directly to large-scale hunting activities (and perhaps to associated features of social organization) are accordingly extremely suspect.

In searching for an explanatory framework to account for the remarkable degree of evolutionary expansion of the human brain, it is also important to determine from the fossil record whether such expansion has taken place uniformly throughout human evolution or whether there have been marked discontinuities. All authors who have taken body size into account in examining the fossil evidence for human brain size evolution are agreed that expansion has been progressive, rather than limited to a short period of geological time, but the exact pattern of rates of brain expansion over time (e.g., uniform versus irregular) remains to be clarified. Such an undertaking will require analysis of data on cranial capacity, estimated body weight and geological age for a large sample of individual hominid fossil specimens. In the interim, one can at least obtain a general picture by considering average values for cranial capacity, body weight and dating for the following taxa: *Australopithecus africanus*; *Homo habilis*; *Homo erectus*; *Homo sapiens* (table 2).

As in other cases, any attempt to "eliminate" the effect of body size through allometric analysis of hominid brain size encounters the problem of defining which is the appropriate level for compar-

TABLE 2
Data on Cranial Capacities and Body Weights for Great Apes,
Fossil Hominids and Modern Man

Species	Cranial Capacity (cc ^a)	Body Weight (kg ^a)	Geological Age (mya)	EQ	EQ _{ow}
1. GREAT APES					
<i>Pan paniscus</i>	325 ^b (N = 8)	35	—	1.94	1.27
<i>Pan troglodytes</i>	385 ^c (N = 363)	40	—	2.08	1.39
<i>Gorilla gorilla</i>	495 ^c (N = 668)	126	—	1.12	0.90
<i>Pongo pygmaeus</i>	405 ^c (N = 442)	53	—	1.77	1.24
2. FOSSIL HOMINIDS					
<i>Australopithecus africanus</i>	442 ^b (N = 6)	30 ^{a-f}	2.8 ^e	3.29	1.90
<i>Homo habilis</i>	642 ^b (N = 3)	40 ^{b,d,e}	2.0 ^e	3.47	2.32
<i>Homo erectus</i>	941 ^b (N = 14)	50 ^{a-f}	1.1 ^e	4.29	2.98
3. MODERN MAN					
<i>Homo sapiens</i>	1230 ^d	57 ^d	—	5.08	3.60

^a Cranial capacities and body weights averaged for males and females.

Sources: ^b Holloway, 1978. ^c Tobias, 1971. ^d Pilbeam and Gould, 1974. ^e Cronin et al., 1981. ^f McHenry, 1976.

ison. Pilbeam and Gould (1974), for example, chose to use the allometric relationship for great apes as the baseline for assessing relative brain size in fossil and modern hominids. As is usual with relatively small taxonomic units (in this case, the family Pongidae), a relatively low value was determined for the allometric exponent ($\alpha = 0.34$ from the major axis). However, this may not be a very appropriate comparison because the largest great ape, the gorilla, is predominantly folivorous and may therefore be expected to have both a relatively low metabolic rate and a relatively small brain size, thus depressing the value determined for the allometric exponent. The data in table 2 have therefore been used to calculate first standard encephalization quotient (EQ) values in comparison to mammals generally, using equation (4), and then Old World simian encephalization quotient (EQ_{ow}) values, using equation (18), in order to assess the change in hominid brain size from two different perspectives (fig. 16). When EQ values are plotted against time for fossil

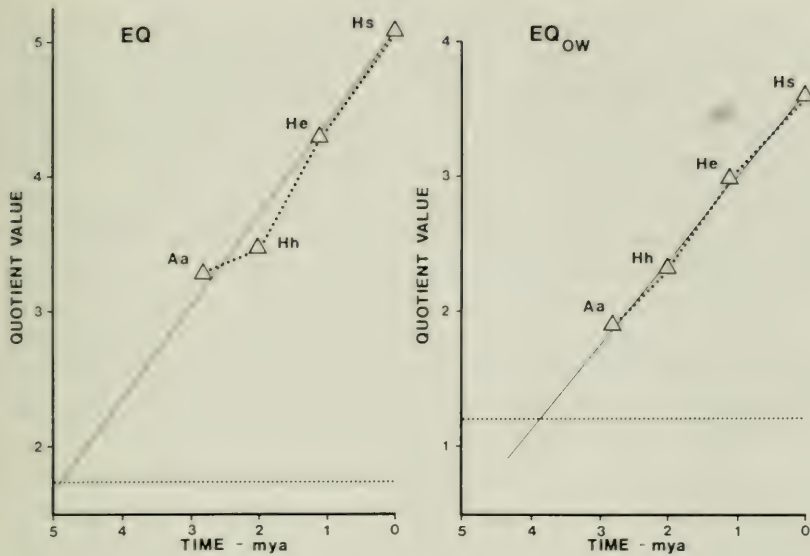


FIG. 16. Plot of encephalization quotient values against time for hominids, using the average values listed in table 2 for cranial capacity, body weight and geological age. EQ values, relating hominid brain sizes to a general placental mammal standard, are calculated according to equation (4) (see also fig. 3). EQ_{OW} values, relating hominid brain sizes to the standard condition among Old World monkeys and apes, are calculated according to equation (18) (see also fig. 12). In both cases, the minimal value for modern great apes is indicated by a horizontal dotted line, while the general trend in the hominid values has been extrapolated back along the best-fit line. [N.B. The lines joining the hominid species need not imply any direct evolutionary continuity; they may merely reflect an overall trend.]

Key: Aa = *Australopithecus africanus*; Hh = *Homo habilis*; He = *Homo erectus*; Hs = *Homo sapiens* (modern).

hominids, it can be seen that *Australopithecus africanus* lies well above both the average condition for mammals (for which EQ = 1.0) and the average condition for great apes (EQ = 1.73), showing a 90 percent increase over the latter. Relative brain size increases progressively above the gracile australopithecine level, but from this perspective there is a suggestion that there could have been some acceleration in brain size expansion following the transition from *Australopithecus* to *Homo*. The plot of EQ_{OW} values, however, shows no such evidence of acceleration in brain size expansion; the data

yield an almost perfect straight line. Since EQ_{ow} values take into account the flatter slope of the Old World simian allometric relationship ($\alpha = 0.60$, as opposed to 0.76 for mammals generally), the quotient value for *Australopithecus africanus* is not so markedly different from that for modern pongids ($EQ_{ow} = 1.20$), but it is still significantly above it and shows an increase of 58 percent over the average great ape value. In both cases (i.e., with EQ and EQ_{ow}) it is possible to extrapolate back in time to estimate when hominid brain size expansion might have started, assuming departure from the minimal condition for modern pongids and no marked acceleration at any stage. The estimates are 5.8 and 4.4 million years ago, respectively, giving an average of about five million years (as was suggested by Jerison, 1973, as a rough estimate). Of course, it is possible that there were in fact significant changes at times in the rate of human brain size evolution, relative to body size, and only additional fossil evidence for the earlier stages of human evolution can resolve this point. For the time being, the following firm conclusions may be drawn:

1. Relative brain size in the earliest well-documented hominid, *Australopithecus africanus*, was already significantly increased compared with modern great apes and therefore considerably advanced over the (doubtless) even smaller-brained common ancestor of great apes and man.
2. Expansion of relative brain size in human evolution has been a progressive phenomenon, though there was possibly some acceleration at the time of transition from *Australopithecus* to *Homo*.
3. Expansion of human brain size, relative to body size, probably began about five million years ago (if not earlier) and therefore antedated all the available fossil evidence of any substance (i.e., anything more than isolated fragments of dubious affinity).

These observations are particularly important in that it is clear that any explanatory framework for the evolution of man's remarkably large brain must account both for the early onset of brain expansion and for its progressive nature. Many discussions of human brain size evolution have been phrased in terms of a direct comparison of modern great apes and *Homo sapiens* and the hypothetical

explanations advanced have tended to imply some relatively abrupt transition associated with the emergence of some special human characteristic. Further, it must be noted that evolutionary expansion of human brain size seems to have petered out about 200,000 years ago, and it has often been noted that classic neanderthals (*Homo sapiens neanderthalensis*) had a larger average cranial capacity than modern man (*Homo sapiens sapiens*). Hence, at a time when human control over environmental resources was presumably moving into its most impressive phase of development, brain size apparently stabilized. This provides additional reason for believing that the progressive expansion in human brain size which took place between five million and 200,000 years ago was a response to relative predictability of specific habitat conditions rather than to man's increasing control over them.

As a final point relating to the fossil evidence for human evolution, it is worth noting that pelvic limitation on increased foetal brain development was probably reached about one and a half million years ago, just prior to the emergence of *Homo erectus*, as currently recognized in the fossil record. Prior to that time, increase in relative brain size above the great ape level could probably have been achieved by modification of the rate and/or extent of foetal growth without any need for significant postnatal postponement of a foetal brain growth pattern. However, subsequent to the attainment of a cranial capacity of about 850 cm³, increasing development of the "secondarily altricial condition," was probably involved as postnatal continuation of foetal growth patterns became progressively more necessary. Thus, it seems likely that increasingly elaborate parental care was required in *Homo erectus* and then still more in *Homo sapiens* to cater for the increasingly helpless condition of the infant during the first months of postnatal life.

CONCLUSIONS

The approach in this discussion of human brain evolution is essentially dependent upon three basic tenets. Firstly, it is taken as axiomatic that no understanding of brain size can be reached without

a consideration of the effects of scaling to body size. Secondly, it is held that only a broad comparative study of brain size in mammals can provide an adequate perspective for reliable interpretation of human brain size evolution. Finally, it is maintained that the obvious heavy energetic cost of brain tissue requires some discussion of the general ecological background to brain size evolution.

Once body size is considered, it emerges that *Homo sapiens* is indeed outstanding among mammals in terms of relative brain size (though the odontocete cetaceans come a close second) and appropriate examination of the available fossil evidence shows that man's very large brain developed progressively over a period of about five million years. To some extent, the pre-eminent position of *Homo sapiens* in terms of relative brain size can be attributed to our primate heritage. We belong to an order of mammals which is marked out by relatively large brains overall, associated with a specific pattern of foetal development in which the proportion of brain tissue at all stages has been increased in comparison to all other mammals. This, in turn, relates to the fact that primates as a group seem to be relatively K-selected and accordingly have precocial, rather than altricial, young.

But *Homo sapiens* has gone far beyond other primates in terms of brain size evolution over the past five million years or more. During this period, we developed a particularly rapid pattern of foetal brain and body development, ultimately complemented by a one-year extension of foetal growth rates into postnatal life, accompanied by the emergence of the "secondarily altricial" condition of the human neonate. We are, in this, unique among the mammals and this should be carefully borne in mind when we consider nutrition during pregnancy and during the first year of postnatal life in comparison with other species. In particular, future improvement in substitutes for human breast milk could well result from specific study of the relationship between milk constituents and early development of the foetal brain. Evidence of possible deficits in brain development associated with the use of milk substitutes deserves particularly close attention.

One enormous question still remains unanswered: Why did this rapid and far-reaching evolutionary expansion of the human brain

take place at all? There is, at present, widespread acceptance of the "savanna hypothesis" of human evolution and a common corollary to this has been the postulate that the large human brain evolved due to specific selection pressures associated with hunting, tool-use and or social organization. Holloway (1973a), for example, sees an important feedback relationship between social organization and human brain evolution: "The human brain is both the product and cause of the evolution of human social behaviour." Yet consideration of the energetic requirements associated with the evolution of the brain, in terms of both the level and reliability of resource availability, must surely place particular emphasis on early human subsistence patterns. *Homo sapiens*, as the most K-selected of the mammal species, must have evolved in response to a rather unusual combination of environmental factors which made available a relatively steady, predictable supply of food lacking in significant toxin levels. Unfortunately, evolution of all the major distinctive morphological attributes of man (large brain; bipedal adaptation; remodeling of jaws and teeth) was well under way some time prior to the earliest known substantial australopithecine remains, so the key evidence is still lacking. However, it can at least be said that an additional, pressing question has now been formulated which will require an answer in future examination of the fossil record of human evolution: "How could hominids afford the energetic cost of developing such a large brain?"

ACKNOWLEDGMENTS

I particularly thank Ms. Ann MacLarnon, who provided invaluable assistance and discussion in the collection and analysis of the data discussed in this paper. I also thank the following people whose helpful comments and advice at various stages contributed to (but in no way makes them answerable for) the analyses and interpretations that have been made: Drs. Leslie Aiello, Este Armstrong, Paul Harvey, Michael Hills, Georgina Mace, Prof. David Pilbeam, Dr. Ben Rudder, Dr. Henryk Szarski. I also acknowledge the major contribution that has been made to the quantitative study of mam-

malian brain evolution by the following people: Dr. Roland Bauchot, Prof. John Eisenberg, Dr. Stephen Gould, Prof. Ralph Holloway, Prof. Harry Jerison, Dr. Walter Leutenegger, Dr. Richard Passingham, Prof. Paul Pirlot, Dr. Heinz Stephan. The special contributions made by Prof. Adolf Portmann, Dr. George Sacher and Dr. Ben Rudder to our understanding of links between reproduction and brain development must also be acknowledged. Thanks are due to Mrs. J. Arnott for typing the manuscript. Finally, I express my considerable gratitude to the American Museum of Natural History for inviting me to give the fifty-second James Arthur Lecture, thus stimulating me to crystallize the above ideas; and the kind assistance of Dr. Ian Tattersall, acting on behalf of the American Museum of Natural History, is gratefully acknowledged.

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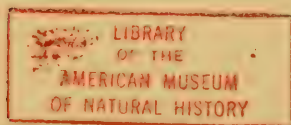
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1984

HIERARCHICAL EVOLUTION OF THE HUMAN CAPACITY: THE PALEOLITHIC EVIDENCE

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JAMES ARTHUR LECTURES ON THE EVOLUTION OF THE HUMAN BRAIN

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- R. W. Gerard, *Dynamic Neural Patterns*; April 15, 1937
- Franz Weidenreich, *The Phylogenetic Development of the Hominid Brain and Its Connection with the Transformation of the Skull*; May 5, 1938
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- John F. Fulton, *A Functional Approach to the Evolution of the Primate Brain*; May 2, 1940
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- **Fred A. Mettler, *Culture and the Structural Evolution of the Neural System*; April 21, 1955
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- **Davenport Hooker, *Evidence of Prenatal Function of the Central Nervous System in Man*; April 25, 1957**
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*Published versions of these lectures can be obtained from The American Museum of Natural History, Central Park West at 79th St., New York, N.Y. 10024.

**Out of print.

†Published version: *The Brain in Hominid Evolution*, New York: Columbia University Press, 1971.

HIERARCHICAL EVOLUTION OF THE HUMAN CAPACITY: THE PALEOLITHIC EVIDENCE

It may seem odd that this annual lecture on the evolution of the human brain is being given by a researcher into the art, symbol, and culture of the last European Ice Age rather than a specialist in the structure and function of the living brain. The fact is that two of the pioneers in the study of the structure and function of the brain in the 19th century, the French paleontologist Edouard Lartet, and the French neuroanatomist, Paul Broca, were pioneers in the early study of Ice Age art and the skeletons and skulls of the early Ice Age artists. Their primary interest in that period of unfolding “natural science” was *man*, man as a species and his evolution. This lecture follows along the path of these two pioneers and will touch on their early work.

Edouard Lartet was a French researcher who, for many years before Darwin published *The Origin of Species*, had been excavating fossils of the extinct animals that once roamed Europe. It was he who first proposed that, as one progressed up the ladder of evolution among the mammals, the brain grew progressively larger in relation to body size and that this trend reached its peak among the primates and man. That finding remains one of the crucial axioms in the modern study of the evolution of the brain (Jerison, 1973). With the publication of *The Origin of Species* in 1859, the possibility presented itself that man may have lived in Europe concurrently with the extinct animals that Lartet was finding. A French amateur archaeologist, Boucher de Perthes, had for decades been digging up hand axes associated with the bones of extinct animals but it was not until 1859, the year in which the *Origin* was published, that these tools of prehistoric man were finally validated. Four years after publication of Darwin's book, Lartet began to excavate stone tools, remains of meals, and bones which had been carved and engraved with animal images in the area of the tiny village of Les Eyzies in southwest France. At a small riverside shelter called La Madeleine, a half-hour by foot from the village, Lartet found in 1864 a fragment of mammoth ivory engraved with an extinct woolly mammoth (Fig.

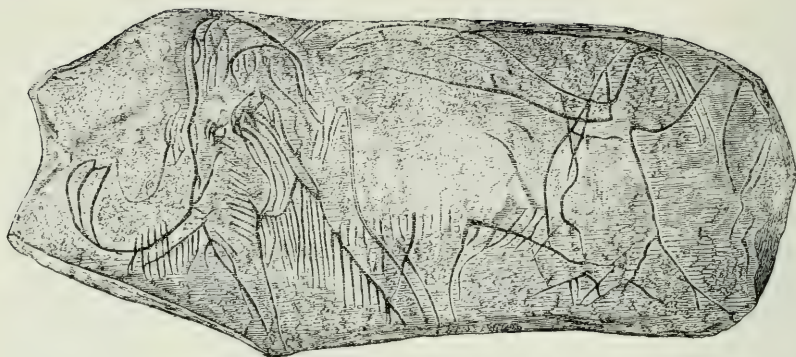


Fig. 1. Engraved mammoth on section of mammoth ivory. La Madeleine, France. Late Magdalenian, c. 11,000 B.C. (after Broca, 1872).

1). That engraving was the first proof that humans capable of making images and art lived in Europe in the time of the mammoth, thousands of years before history began. Lartet spent the rest of his life excavating the sites of early man in the Les Eyzies area. His work with the Englishman, Henry Christy, gave us the first body of Ice Age art, at once raising questions concerning the relevance of this early art and symbol to these prehistoric cultures and the evolution of man. In 1867 and 1868, Lartet was elected secretary of the first two International Congresses of Anthropology, held in London and Paris. He was one of the founders, then, of several disciplines, including modern paleontology and the comparative study of evolution of the brain, Ice Age archaeology and the study of Ice Age art, and of French anthropology, or the study of man in general.

In 1861, shortly before Lartet began excavating at Les Eyzies, his colleague, the neuroanatomist Paul Broca, delivered a paper to the French Society for the Advancement of Science, announcing one of the crucial analytical discoveries in the study of the human brain. Broca had examined the brain of a deceased patient who had previously lost the capacity to talk and he found that the loss of speech had been caused by a lesion in the frontal lobe of the left hemisphere. That finding, concerning what is today known as “Broca’s area,” began the study of localization of brain function, left-hemisphere dominance for language, and left/right hemisphere asymmetry—



a, Tayac Church.

b, Les Eyzies Railway-station.

c, Cro-Magnon Cave.

d, Rock of Les Eyzies.

e, Château of Les Eyzies.

f, Railway-bridge across the Vézère.

Fig. 2. The village of Les Eyzies at the foot of the limestone cliff, with the railroad bridge that was being built when the Cro-Magnon skeletons were found (after L. Lartet, 1875).

studies that are still the bedrock of inquiries into higher brain function. Broca had also begun the histological analysis of brain tissue, one of the major techniques for research in comparative brain differences and the localization of specialized function. At the end of his life he made another major discovery, this time not about a function of the higher cortex, but about a portion of the lower sub-cortex. He located and named the system found just below the cerebral cortex in all animals, including man, the “limbic” system. In recent years this area has received popular designation as the “old mammalian” or “visceral” brain (MacLean, 1973). It has undergone increasingly precise reductive analysis at the cellular, molecular, and functional levels and its popular designation as the “mammalian” brain has changed as its role in higher cortical function has been elaborated. In man the limbic system has been found to be important in memory, selective attention and emotion, and it has functional connections to the cortex, including parts of the frontal lobes and the language system, which still need to be clarified. It is this set of findings, concerning early man, his art, his capacity, his culture, and his brain, that we will discuss today.

In 1868, the French government was building a railroad from Paris to the isolated farm areas around Les Eyzies. Landfill was needed to build a railroad bridge across the Vézère River, on which the village sits pressed against a high limestone cliff (Fig. 2). In

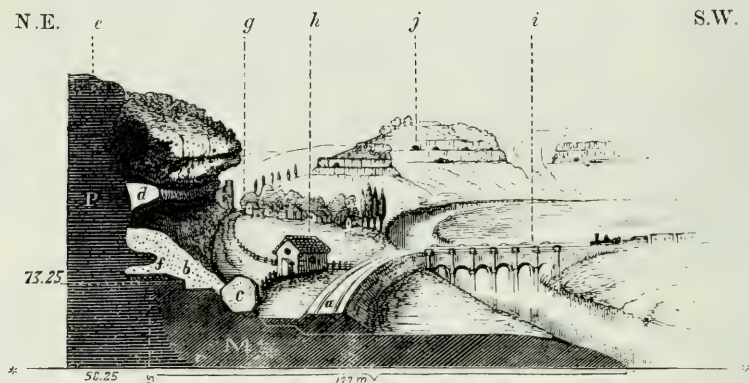


Fig. 3. The cave of Cro-Magnon, uncovered while digging for landfill for the Les Eyzies railway bridge (after L. Lartet, 1875). Abbreviations: a, railroad; b, talus; c, great block of stone; d, ledge of rock; e, rock of Cro-Magnon; f, cave; g, château and village of Les Eyzies, in the valley of the Beune; h, gatekeeper's house; i, railway bridge over the Vézère; j, Caves of Le Cingle. P, limestone; M, detritus of the slopes and alluvium of the valley.

digging for landfill at the base of the cliff (Fig. 3), the workers uncovered a cave containing the skeletons of the makers of the tools and art that Lartet had been finding in the area. With the skeletons, in fact, were incised images and necklaces of seashells that came from both the Atlantic and the Mediterranean. Lartet's son, Louis, was commissioned to verify the authenticity of the excavation. Broca was given the skeletons of Cro-Magnon to study. I quote from the paper that Broca read to the French Society for the Advancement of Sciences in 1872.

The skeletons of these robust troglodytes (or cave-dwellers) bear traces of the violence of their manners; in the lower extremity of one of the femurs of the old man is a hollow similar to that produced in our day by a spent ball. It is evidently the result of an old wound received, perhaps, in the chase; perhaps in war; but a human hand, armed with a flint instrument, must have produced a long, deep aperture which appears in the skull of the woman (Fig. 4); the width of the opening shows that the brain must have been injured, but still the victim was not killed instantly . . . the skull shows that she survived about 15 days . . . The troglodytes of Cro-Magnon were then savages, but savages of intelligence, capable of improvement . . .

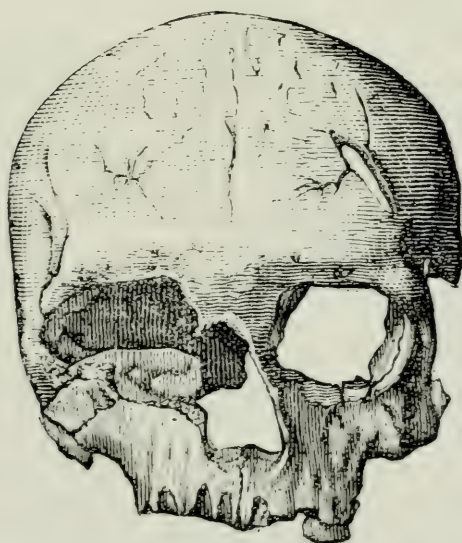
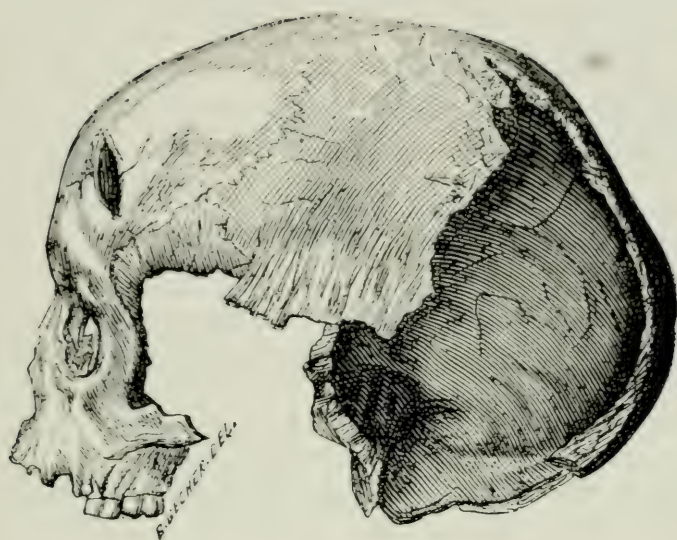


Fig. 4. The skull of the Cro-Magnon woman showing the deep cut (after Broca, 1872).

I do not know if Broca meant “improvement” to modern historical standards, since in the realm of violence that would not constitute a great improvement. But Broca continues:

We find among them (the Cro-Magnons) certain signs of a powerful cerebral organization. The skulls are large in diameter . . . and capacity and surpass the mean of . . . existing races The amplitude of the frontal compartment denotes a great development of the anterior cerebral lobes, which are the seat of the most noble facilities of the mind The conformation of their brains show that they were capable of culture These rude hunters of the mammoth, the lion and the bear are the worthy ancestors of the artists of La Madeleine

The Cro-Magnon skeletons of the early Ice Age, c. 28,000 B.C., were some 17,000–15,000 years older than the incised mammoth from the later Ice Age found by Lartet at La Madeleine.

Broca’s discussion of the spear wound in the woman’s skull makes no mention of the limbic or other subcortical systems which participate in human reactions of violence, anger, and killing as well as aspects of the capacity for spatial orientation and memory. In fact, Broca was not to discover and name the limbic system for some years, and even then he would not understand the extraordinary functional complexity of the system which, more than a century later, is still under investigation.

We must be cautious, then, of too simplistic an explanation of the apparent wound in the skull. Perhaps the killing was not “limbic,” but had major input, motivation, and rationalization coming from higher levels of brain function; perhaps it was the result of a ritual or ceremonial act, a sacrificial killing, an act of “justice” carried out, or the result of superstition concerning witchcraft or the breaking of a taboo by that woman. We do not know. We know only that we are dealing with *man* and in man the brain mediates cultural as well as reactive, subcortical responses such as anger and aggression.

In the century since the discovery of the Cro-Magnon skulls, while Broca’s analysis was forgotten, archaeologists have uncovered evidence that the symbolism of death and killing goes back at least to the Neanderthals, 100,000–35,000 B.C., and perhaps to the still earlier human known as *Homo erectus*, c. 400,000–300,000 B.C. The Neanderthals not only buried their dead with symbolic artifacts, including red ochre, animal bones, and flowers, but apparently both

killed and symbolized the dead. At Mount Circeo, in Italy, workmen dug into a limestone hill to enlarge an inn and discovered a cave in which there lay a Neanderthal skull surrounded by a circle of stones. The skull had "one or more violent blows on the right temporal region that had caused conspicuous damage to the frontal and temporal lobes and the zygoma. This mutilation points to a violent death, probably a ritual murder. The other mutilation consists of the careful and symmetric incising of the periphery of the *foramen magnum* . . ." (Blanc, 1961). Still earlier human skulls from Europe show a similar widening of the *foramen magnum*. At the *Homo erectus* cave site of Peking Man, at Choukoutien, China, c. 400,000 B.C., the fragments of 40 human skulls were found with only a few limb fragments, suggesting some level of choice or symbolization. Recently, a far earlier hominid skull was found, in Bodo, Ethiopia, that had cut marks made with a stone knife below the left eye socket and on the frontal bone, suggesting intentional removal of the skin from the face and head. Whether this was an act of limbic "aggression," an act of "cannibalism," or a symbolic act of "sharing" in the spirit or person of the deceased (and therefore an act of reverence), we cannot tell. But in any case, it involved an intentional act related to the death of a conspecific that may have had an element of symbolic, if nonlinguistic, meaning.

Whatever aspects of the symbolism of killing and death that did exist in the cave at Cro-Magnon were apparently prepared for in earlier periods of human evolution and culture. In all such early instances, it was not the aggression and violence that were significant but the possible beginning acculturation and symbolization of the act or process of killing and the uses of death. One of the findings of the present program of research into Ice Age art and symbol is that images and uses of death had become extremely variable and complex by this period. With this introduction, we can turn to an analysis of certain specialized aspects of Ice Age art and symbol, the only body of materials in which the full range of higher cortical function is evident.

During the last Ice Age, one-half of Europe was covered by a sheet of ice a mile and more thick. Half of Germany, England, and all of Scandinavia lay under the ice sheet. So much water was locked up in ice that one could walk from England to France. During this

period the Cro-Magnon hunters lived primarily along the network of rivers that flowed from the great ice sheets and the mountains and hills, either westward to the Atlantic, or south to the Mediterranean and Black seas.

When I began my research some 20 years ago it was held that modern *Homo sapiens* had walked into Europe some 35,000 years ago, displacing the Neanderthals who had lived there for the previous 75,000 years. These Cro-Magnons carried a new skeleton, a new tool kit involving a large use of bone, and the first art to be found anywhere on earth. These beliefs have changed during the period of the present research.

I present the analysis of some examples of Ice Age art excavated in this century. The carved horse of mammoth ivory, only 2½ inches in size, is the oldest animal image known (Fig. 5). It is 32,000 years old and comes from the early Aurignacian, the period of the Cro-Magnon skeletons, but it is nevertheless some 2000–3000 years older than the skeletons. It was found at the small habitation cave of Vogelherd in Germany.

The first thing to note is that, though this is the earliest example of representational art known, it is not “primitive.” It is, in fact, extraordinarily sophisticated. This is not the way the Ice Age horse looked, for it was short, stocky, and had a thick muzzle and neck and a stubby body. The image, therefore, is an abstraction of “horseness,” depicting the characteristic movement and feel of the species. This capacity to abstract an image, form, and species character, was, as we shall see, one of the crucial nonlinguistic, adaptive, symboling capacities of the early human cultures.

When I began my research, such animal images from the Ice Age were generally considered to be aspects of “hunting magic.” It was assumed that Cro-Magnon, as a hunter, made an animal image, went through the act of “killing” the image, and by this act of sympathetic magic, went out and hunted with greater assurance of success.

When I put the carved horse under the microscope, data contradicting this view emerged. The eyes, ears, nostrils, mouth, mane, and tail had been carefully carved, but these were worn down and polished from long handling. Since this was ivory, the handling involved, if the statue had been taken in hand periodically for use

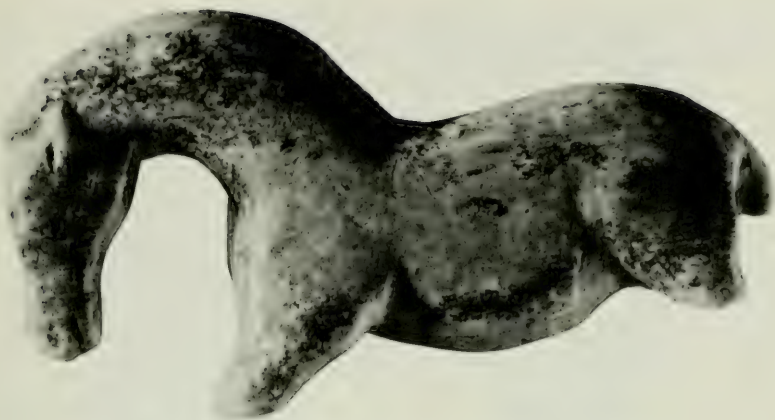


Fig. 5. Ivory horse from Vogelherd, Germany, c. 30,000 B.C.

in ritual or ceremony, could have extended over a number of years. At one point in its use an absolutely fresh angle or “dart” had been incised in its shoulder. The dart or wound seemed to represent a late use or “killing” of the horse image. We do not know whether this “killing” was for a curing, a birth, a death, a shamanistic initiation, or perhaps the coming of spring. The evidence of long use and of a single, late, specialized “killing” indicate that the horse was not merely the image of a meal. It was a symbol, made to be used over time in different ways, *one* of which involved a symbolic killing. This “killing” was not subcortical and reactive, but was a cortical, cultural act, probably performed without rage or the impetus of hunger. I have documented the fact that the variable, periodic use of an animal image involving renewal, killing, and association with a range of signs, represented a primary mode in Ice Age art (Marshack, 1969, 1972a, 1972b, 1984b). The variable use of a generic symbol over time, in a range of contexts, represents a modern human mode. It is different from the recent use of images and signs as one-dimensional signifiers in the “proto-language” experiments conducted with chimpanzees and gorillas.

The engraved horse, in fact, was extraordinarily complex. As a carved symbol and image it was, in part at least, a product of right-hemisphere function, since that hemisphere is normally involved in

image formation and in spatial, three-dimensional evaluation. But the long-term, periodic, and specialized use of the horse involved the frontal lobes, which function in cultural planning and in the motivation, maintenance, and evaluation of cultural schedules and behaviors. Simply as a carving, it was the product of another basic capacity of the species, the vision-oriented, *two*-handed capacity for problem solving (Marshack, 1984a). While it was being carved, one hand, presumably the right, engaged in the complex, shifting sequence of carving, while the other, presumably the left, engaged in holding, orienting, and turning the ivory as it was being carved. The right hand manipulated a series of specialized tools in the sequence of cutting, scraping, engraving, and polishing, while the left hand maintained the object in proper orientation, at the correct distance, and with a continuously changing counterpressure to the work of the right hand. From the beginning to the end of the carving process, including obtaining the ivory and the flint for making the stone tools, the essential problem-solving, productive sequences were nonlinguistic. We do not know what level of language accompanied the making and use of the horse, but we can assume that it was sufficient to explain its meaning and use.

The same complexities are involved in other aspects of Ice Age art. The famous "Venus" of Lespugue, c. 25,000 B.C., was excavated in France and appears somewhat later than the Cro-Magnon skeletons (Fig. 6). We have, again, an image of great sophistication, containing an almost modern, 20th century shape and form. This is not the image or portrait of a real woman, but an abstraction and schematization of femininity or "womanness," in much the way that the prior carving was an image of "horseness." The carving has exaggerated breasts, hips, and vulva, with tiny hands and feet and no face. Microscopic analysis of the wear, polish, and different types of overpainting and overmarking on the Venus figurines has shown that they, too, were often intended for long-term, periodic, and variable use. In addition, as a generic symbol, they apparently embodied a range of meaning that varied with each use—concepts relating to fertility, the onset of menarche, birth, the periodicity of menstruation, the dangers of delivery, and the process of lactation. There is also evidence that they were related to the periodicities of flora and

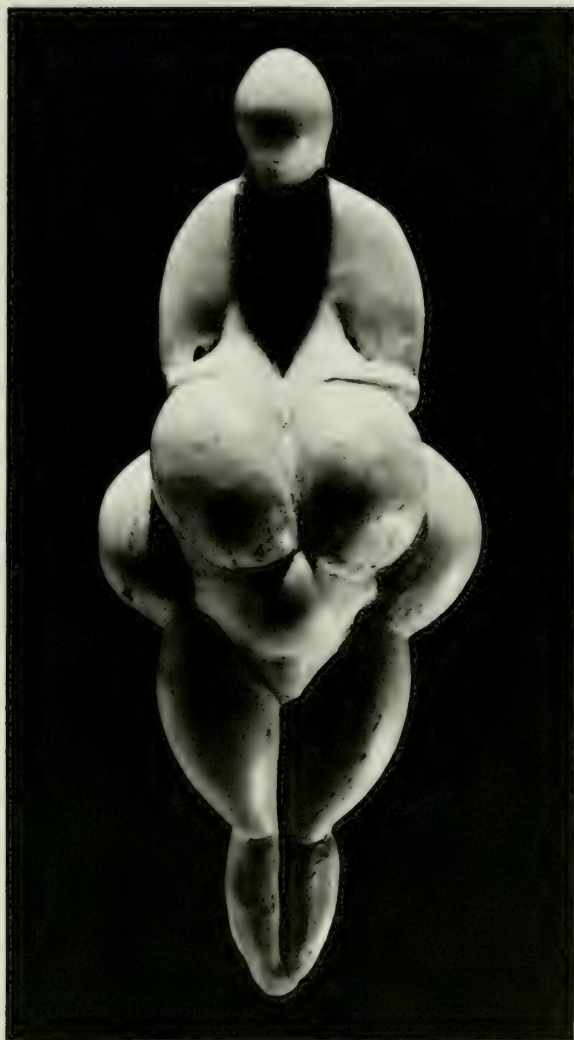


Fig. 6. Ivory statuette of female, the famous "Venus" of Lespugue, France, c. 25,000 B.C.

fauna and in some forms seem to be "ancestor" figures. We are dealing, therefore, not with "art" or representation, but with a core, multivalent symbol. It may therefore be of significance that these



Fig. 7. The village of Les Eyzies as it looks today. Front houses are on the valley floor, houses against the cliff are on a shelf overlooking the valley. Harvard University office is building on shelf at left.

symbolic females were treated differently from the Cro-Magnon woman who, while alive, had apparently had a spear thrust into her skull. Different, that is, in the sense that none of the Ice Age female figurines, were ever symbolically “killed,” though we have evidence of their variable use.

The same two-handed, vision-oriented skills involved in making the horse were involved in making the figurine, though the reasons for making each differed. In each case the productive skills, symbolic processes, and motivations involved were nonlinguistic. The relations of these two-handed, vision-oriented symboling skills to the evolutionary processes involved in hominization and the subsequent origins of language and art, must, therefore, be touched on. To do this I return to the village of Les Eyzies, for that village and its valley were part of the reality and context within which eyes, hands, symbols, and language functioned.

This is Les Eyzies as it looks today, photographed from the bank of the Vézère River (Fig. 7). Ice Age man lived on the high shelf below the limestone overhang. The building at the left is the Harvard University office for the excavation that was under way just behind the house, the Abri Pataud. That excavation, conducted by Hallam Movius, went down to the early Cro-Magnon period of about



Fig. 8. The valley of Les Eyzies as it looks today. The Vézère River below, with the 19th-century railroad bridge. The equinoctial point on the horizon is just to the right of the large farmhouse across the valley at right. The winter solstice sun sets to the left of the smaller set of farmhouses, where the cattle graze. The summer solstice sun sets at far right, out of the picture.

28,000 years ago. The cave of Cro-Magnon itself is about 40 or 50 yards to the left and is now the site of a Michelin starred restaurant and hotel. In the last few years, archaeologists digging at the foot of the rock fall or talus below the cliff have found the tools of Neanderthal man. The cliff shelf above the village may, therefore, have been occupied more or less continuously for some 40,000 or 50,000 years. Not many kilometers from Les Eyzies, and within walking distance of this cliff, earlier examples of man or his artifacts have been found, going back to the period of late *Homo erectus* of about 300,000 years ago. The late evolution and transition to modern man was in large part lived out among these valleys and hills, as it was in other areas.

Figure 8 is a view of the valley as seen from the shelf, standing in front of Harvard's Abri Pataud office. The shelf is oriented due west toward the hills across the valley, the shelf itself running true north and south. Crossing the river is the railroad that was being built when the Cro-Magnon skeletons were found more than a cen-



Fig. 9. Polychrome painting of so-called "Chinese horse" from the cave of Lascaux, France, not far from Les Eyzies, c. 14,500 B.C. Horse is in its summer coat.

tury ago. In the distance across the river, the tiny specks around the farmhouse are grazing cows. Their small size represents the way the browsing herds of bison and horse would have looked during the Ice Age. Inside the limestone hills that form the valleys of the region one finds the caves and the paintings that have in this century become famous as the primary products of the Ice Age cultures. These paintings represent a later tradition than is documented in the Vogelherd horse and the "Venus" figurines. The famous, so-called "Chinese horse" from the cave of Lascaux, not far from Les Eyzies, is dated at about 14,500 B.C. (Fig. 9). Like the earlier carved and engraved animal images, these painted images were originally called "hunting-magic," and for that reason the signs and symbols around the horse were presumed to be weapons and traps. More recently, Freudian interpretations of the long signs as "male" and the wide as "female" have been attempted. We shall look shortly at what these signs really mean and how they relate to symboling modes of the brain.

I first came to Les Eyzies about 20 years ago at the beginning of

July. Professor Movius and I stood on the shelf looking across the valley as the sun went slowly down behind the hills far to the right, sinking as a great red disc. As it was going down, the first crescent of the new moon appeared in the sky as a thin silver arc, facing the sinking sun. It was instantly apparent that the Les Eyzies horizon formed a perfect natural "calendar" and that the first crescent would appear over those hills at sunset every 29 or 30 days. It was also apparent that the sun was sinking at its farthest point north on that horizon, its position at summer solstice, and that it would now begin to move south until it reached a point at which the Vézère River exited the valley between the hills, on its way to the Atlantic. The visual effect of the silver first crescent, aiming its arc at the setting sun and following the summer sun down, was stark and dramatic. There was no way that generations of hunters living on that shelf over a period of 18,000 years or more could fail to notice these periodic changes and movements of the sun and moon. They would have noticed these changes with or without an explanatory use of language, particularly since these visual periods also marked the patterns of faunal and floral changes occurring in the valley. Such observations are well known amongst the world's hunter-gatherers and have been profusely documented in this century. It took the next 18 years, however, before I could properly put together the seasonal and ecological dynamics of that valley and work out its relations to the art, images, and paintings in the caves and to understand the adaptive contents and uses of the art. At the end of the inquiry, I found that I was investigating the hierarchical cross-modal complexity of the evolved human brain and was also inquiring into the adaptive role of symbol, both in language and art. The questions had been incipiently implied, but had never been directly raised, by the pioneering work of Lartet and Broca. I return to the valley.

The Vézère River flows westward to the Atlantic, exiting some 150 miles to the west, in the estuary beyond Bordeaux. The river flows south at Les Eyzies and turns west between the hills at the end of the valley. When the setting sun reaches this low point at the winter solstice, we are in mid-winter, the days are short, and the sun sets early. From the winter solstice on, the setting sun begins its march back toward the north. When it reaches its midpoint on the

horizon, it is the time of the spring equinox around March 21. The winter was over and the thaw and flood were about to begin. This was only some three or four first crescents after the first frosts or snows had descended on the valley. A few weeks after the thaw, the Atlantic salmon began to come up river on their yearly spawning run, arriving by the thousands. They spawned in the many small tributary streams of the Vézère, one of which, the Beune, flowed into the river at the foot of the cliff where the hunters camped. That spring run of salmon would have represented the first large availability of fresh meat after the hardship of the winter.

At about the same time, a few days or weeks after the thaw, the reindeer would have begun migrating through the valley, arriving from the lowlands toward the westward coast and heading for the cool hills to the east, behind Les Eyzies, for summer pasture. The herds would probably have crossed the Vézère at the point where the railroad bridge stands, since it is built on a low point in the river created by a natural geological fault and ford (White, 1985). The arrival of salmon and reindeer, when the setting sun was at midpoint on the western horizon, marked the beginning of the abundant half-year. Six months later, at autumn equinox, a few weeks after the sun had again reached that midpoint, the reindeer herd would come back across the river, this time heading west, for lowland pasturage without troubling insects. It was probably at this crossing point and time that the Cro-Magnon hunters of Les Eyzies killed the summer-fattened reindeer, not only for their meat and fat, but for their fall skins and their autumn antlers. The reindeer were not only food but a major resource of working materials and hides. Throughout the year other animal species would also have been moving through the narrow river valley or on the flat plateau above, following the shifting availability of plant growth.

About 10 minutes by foot up river from Les Eyzies, on the other side of the river, is a site that Lartet first excavated in the 1860s, a habitation cave in the small Gorge d'Enfer. A tributary stream flows through the gorge. Carved on the ceiling of the small cave is a 3-foot-long salmon, a clearly represented male salmon at the time of the spring run with the typical hook or "kipe" on the lower jaw that is found only on the male at this period. I have published this image

of the male salmon from many Ice Age sites, including those north of Les Eyzies and those as far south as the Pyrenees (Marshack, 1970, 1972a, 1975, 1985a).

It was in the Gorge d'Enfer that Lartet excavated an unusual bone plaque marked on both faces with sets of dots and lines (Lartet and Christy, 1875). It was this plaque that initiated my own investigation of the cognitive content in the early Ice Age symbol systems. The plaque was originally published as a possible "tally," presumably of animals killed. When I first came to France to begin my inquiry, it was to study this strange plaque and the others like it that had begun to be found in all periods of the Ice Age. We shall analyze one shortly.

Downriver from Les Eyzies, about a half-hour drive by car, the Vézère enters the Dordogne, which then flows toward Bordeaux and the Atlantic. At the junction of the two rivers there is another shallow area, or ford, where reindeer herds crossed during the Ice Age. Overlooking the ford was a habitation site on a hill called Limeuil. Here, engraved on broken pieces of limestone that had fallen from the shelter wall, over a hundred images of reindeer and other animals were found. These depict the differences in male and female reindeer at the time of the spring and autumn migration; they include spring calves, the male reindeer in the autumn with a full head of antlers, head up, mouth open, braying in the time of the autumn rut. It is a few weeks after the autumn rut that the male drops his antlers, while the female retains hers through the calving in the springtime in order to protect the calves. These differences were all depicted. Again, I have published a large body of such images depicting the sexual and seasonal characteristics and behavior of different species in the art of the Ice Age (1970, 1972a, 1975, 1985a).

It was Lartet who had begun the consistent excavation of these animal images, as well as the tools and the remains of meals. But it was his so-called "tally" that had initially intrigued me. About 15 or 20 minutes upriver by car from Les Eyzies, at a riverside site called the Abri Blanchard, a small plaquette was found in the 1930s that was similar in size and shape to the one found a short distance away by Lartet in the Gorge d'Enfer. This plaque and the one from the Gorge d'Enfer were lying together in the Musée des Antiquités National, outside of Paris, when I began my studies. They both came



Fig. 10. Carved bone plaque from the habitation site of Blanchard, France, not far from Les Eyzies, c. 28,000 B.C. The surface has a sequence of marks determined to be notational.

from the same early period of the Ice Age as the Vogelherd horse, the “Venus” figurines, and the Cro-Magnon skeletons.

The Blanchard plaque (Fig. 10), originally published as a “polisher,” was presumably intended to smooth leather and was decorated with what was described as a meaningless or random pocking. Microscopic analysis revealed that it was not a polisher and that it was not decorated. Instead, the analysis revealed that it represented the most complex single problem-solving artifact of that early period of human culture. The plaque (10 cm long) was just large enough to be held in the hand. It had high polish at the rear where it had pushed against the palm, but it was broken back at the front by persistent pressure occurring during the fine retouch of flint tools. It was, then, a pressure flaker and the amount of polish in the rear and frontal breakage suggested that it had been used for a considerable period, perhaps of some months. Microscopic analysis further revealed that the pocking in the small center area (4.4 cm) was in reality an accumulation of 69 marks that was broken down into 24 *sets* of marks, ranging from one to seven units each. Each set was made by a different tool or point and with a different type of stroke, some punched, some arcing to the right, some to the left (Marshack, 1970b, 1972a, 1972b, 1975).

The analysis revealed that the accumulation began in the center

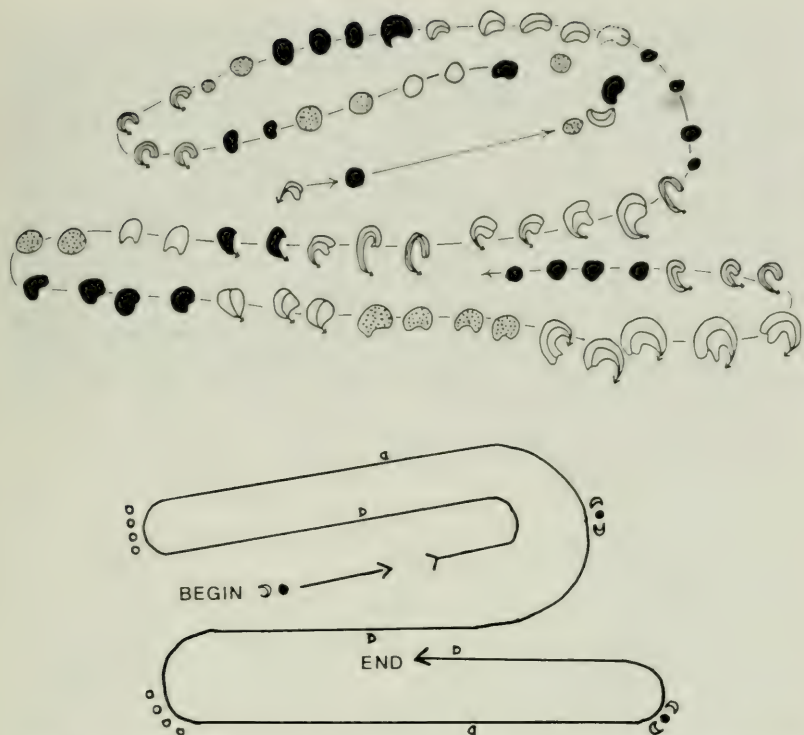


Fig. 11. Schematic rendition of the incised marks on the Blanchard plaque. The 69 marks are made in 24 "sets" in different styles and by different tools, forming a serpentine image that models the waxing and waning of the moon.

of the marking and proceeded set by set in a serpentine manner, with two turns occurring at the left and two at the right (Fig. 11). Because of the many changes of tool and stroke, the accumulation of sets had clearly occurred over a period of time. It was apparent, therefore, that this was some form of notation, made some 20,000 years before the invention of formal recordkeeping or writing in the later agricultural civilizations of the Middle East. Internal analysis of the sequence indicated that the Blanchard engraving apparently represented a nonarithmetic, observational lunar notation covering a period of $2\frac{1}{4}$ months, with the turns occurring at the major changes of phase in the lunar month. All the full-moon periods fell to the

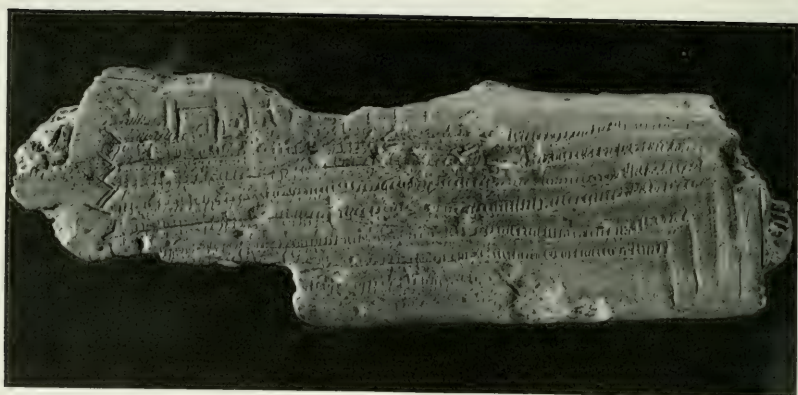


Fig. 12a. Bone plaque from the Grotte du Tâi, France, incised with a sequential, boustrophedon notation. Terminal Magdalenian period, c. 9,500 B.C.

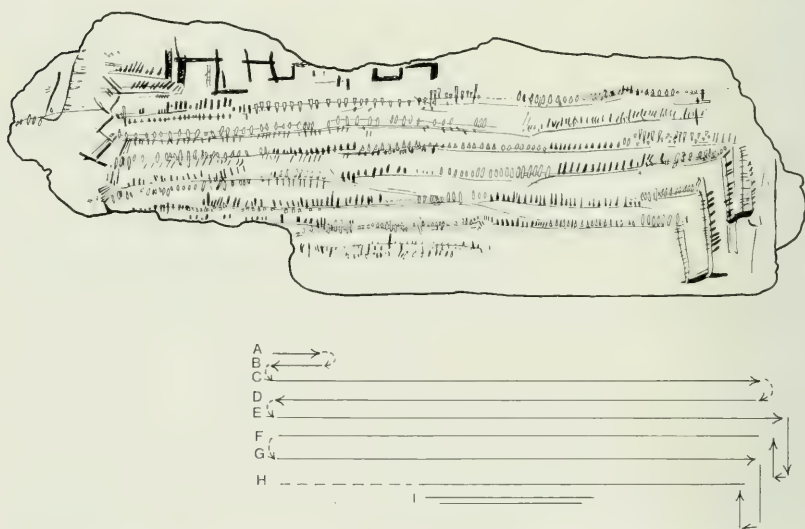


Fig. 12b. Schematic rendition of the marks on the Grotte du Tâi plaque, indicating the subsections and the marking on the descending lines at the end of rows E-F and G-H.

left; all the periods of crescent moon and invisibility fell to the right; and the half-moons fell in midline.

Cognitively, within a single artifact, we had two types of “tool,” one practical and one conceptual or ideational, each of which func-

tioned differently and with different patterns of neurological specialization. This mode of creating multiple and variable functions in a single artifact is well known among hunter-gatherers. The Blanchard plaquette had apparently been made by someone who carried it about as a portable item, perhaps in a pouch, to be used for sharpening or shaping stone tools and during that period had used the available surface for notating the passage of time. The plaquette found by Lartet in the 1860s, on the same river and just a few kilometers away, was of the same type, except that the engraver had made use of the edges as a containing line for his sets and had therefore accumulated them in a somewhat different manner (Marshack, 1972a, 1972b, 1972c). It was the analysis of the Blanchard plaque early in the research, and the analysis of the one from the Gorge d'Enfer which also contained the springtime image of a male salmon in the time of spawning, that provided an early clue as to the possible relationship of the animal art of the Ice Age, with its developing realism and its descriptive sexual and seasonal detail, to the calendric notations. The notations and the animal images functioned as interconnected referential symbolic modes.

The Blanchard plaquette was engraved at the beginning of the last Ice Age, c. 28,000 B.C. Some 18,000 years later, at the end of the Ice Age, when the climate was warming, when the mammoth had disappeared from Europe, and when the hunting-gathering cultures of the Ice Age were on the verge of drastic change, a similar plaque was engraved at another site in France (Fig. 12a). Excavated in the 1960s, the engraving was so complex that, after I had developed the microscopic method, the excavators requested I come to France to study it.

Microscopic analysis revealed that the plaque (8.6 cm long) from the Grotte du Tâi was originally a working tool, perhaps a pressure flaker, that had been broken at the left. It had then been cut at the right and a bit of bone had been snapped off, not quite cleanly, to make a small, portable slate that could be used for marking. At first glance it seems that the plaque is incised with nine or ten horizontal lines (A to I on Fig. 12b). Microscopic analysis of the engraving, however, revealed that these were not single horizontal lines, but that each horizontal was composed of short sections, one appended

to the other and often overlapping. Each of these subsections was marked with its own set of tiny marks. Analysis of the marks in each subsection revealed that they were made by different tools and with a different rhythm of marking from that of adjacent subsets. Some sets were incised upward and some downward. There were other indications of cumulative marking. At the beginning of a row there tended to be ample space for the marks, but as the accumulating sets approached the end of a horizontal row, they began to crowd together, as though the engraver had run out of needed space.

At the far right, near the break, there were two right-angle descents. They occurred at the ends of rows E-F and G-H. Each of the descending lines was connected to an ascending line by a horizontal bar, and both the descending and ascending lines had been incised with sets of tiny marks. Apparently, the engraver had not planned well, for extra marking space was needed at the end of row E to complete a marking sequence to a certain required length. Having added a descending line, the engraver was forced to take account of the lack of horizontal space for the next set of rows (G-H) and do the same. This was not the way a "decoration" would have been marked. We had, in fact, found a problem-solving strategy that provided a clue to the direction and mode of marking. The marking represented a serpentine or boustrophedon notation that was conceptually in the tradition of the earlier Blanchard plaquette. This main face notated $3\frac{1}{2}$ years, 6 months on each long horizontal, with the turns coming at the solstices. On the reverse face there were additional sequences of notation marked on horizontal subsections, totaling approximately 5 to 6 months (Marshack, 1973).

The two-handed, vision-oriented capacity and the cognitive, spatial, observational, and notational problems to be solved were similar in the Blanchard and the Grotte du Tâi notations, except that we have evidence of a developing complexity during the 18,000 years between the two. By the end of the Ice Age, the notation of lunar periods and months had been extended to the marking of a longer, more inclusive lunar-solar "year" as a relevant concept. I assume that by the end of the Ice Age the "year" as a conceptual frame had become practically, ritually, and mythologically signifi-

cant in Cro-Magnon culture and I have begun to document the nature of that historical development elsewhere (Marshack, 1984).

Here I wish to examine a few of the hierarchical neurological capacities involved in the notations and to inquire into their relevance for our understanding of the selective evolution occurring within the human brain for certain types of cross-modal, associational function, involving vision, tool use and manipulation, abstraction, sequencing, and image formation. Both notations were a product of the evolved, two-handed, vision-oriented capacity for variable problem solving. The strategies evident in the two plaques, however, were of different types and occurred at different levels of reference and abstraction.

When the Blanchard plaque was being used as a pressure flaker or retoucher, each hand was engaged in a different set and sequence of problem-solving strategies. These involved separate sensory perceptions and a differentiated manipulation and handling of the objects held in the right and left hands. The process involved continuous feedback and evaluations and judgments of the different ongoing actions of each hand. The total process, mediated at both the tactual and visual levels, was being cojointly evaluated at subcortical and at right- and left-hemisphere cortical levels. Presumably, the right hand, grasping the plaque as a pressure flaker, performed the specifying action of chipping or flaking the flint tool being held in the left hand. The left hand, holding the flint to be sharpened, was carrying out the orienting and grasping action, shifting and turning the flint as it was being worked, and with each specifying action of the right hand, providing the proper measure of counter pressure for the bone flaking tool. Watching a toolmaker at work during pressure flaking would make it clear that two separate but coordinated strategies and sequences of motor skills are being performed by each hand.

The two-handed, lateralized, vision-oriented, and tool-mediated skills involved in working a piece of flint are, in general, similar to the two-handed problem-solving skills involved in carving a chunk of mammoth ivory into a horse or figurine. The intent and problem-solving strategies, however, are different. In carving an image, a

changing set of flint tools is held in the specifying hand and it is the ivory, held in the other hand, that is being worked or shaped. In pressure flaking it is the bone that is held in the specifying, dominant hand and it is the flint that is being shaped. The same hands, eyes, and brain mediate both sequences, but the strategies are different and are intended to achieve different ends. When the bone was used as a pressure flaker, the intent was to achieve a utilitarian cutting edge. In the case of the carvings, the intent was to produce a non-utilitarian, symbolic artifact whose meaning was in the form. When the bone was used as a pressure flaker, it was a secondary tool being used to make a primary tool, the cutting edge. The skills involved in creating a cutting edge go back at least to the early hominid, *Homo habilis*, of some 2.5–3 million years ago, when the first crude pebble tools were made by use of a hammerstone held in the preferred hand, knocking off flakes from a pebble, probably held against the ground by the secondary hand. The use of a bone hammer or pressure flaker for the fine retouch of an edge appears to have begun with *Homo erectus*, some 1–2 million years ago. The brain and two-handed capacity had by then evolved, as had the range of tools, tool use, and materials being worked. Though there was now a qualitative difference in the capacity of the two hands, the essential two-handed problem was the same as that for the chipping of the pebble tools. Therefore, as a fine retoucher, the Blanchard bone stood at the end of a long neurological and cultural development.

When the Blanchard bone was being used not as a pressure flaker, but for *notation*, however, the hands and the problem were reversed. The bone was now probably grasped in the *secondary*, nondominant left hand, while a flint engraving tool (which may have been shaped or sharpened by the same bone plaquette), was now being held in the right hand, where it served as a stylus for incising an accumulating sequence of abstracted units or sets. This notation was not writing, since the units and sets were nonlinguistic, and it was not arithmetic since the sets and the combination of sets, though quantitative, were not counted or summed. Nevertheless, the problem-solving processes involved in structuring and sequencing a notation, were of the same order as, and incipient to, those that would be found in the later development of writing and arithmeticized rec-

ordkeeping. In the Cro-Magnon cultures of the European Ice Age the social need and the historical preparation necessary for formal writing and arithmetic were not yet present.

I now go to a different level in our analysis of the hierarchy of variable cortical functions apparent in the Ice Age notations. The Blanchard notation was accumulated in a serpentine manner with the “turns” coming at the two points of major observational change in the lunar month—the period of the full moon and that of the crescents and invisibility. I assume that the image was created as a result of the *ad hoc* problem solving faced by the engraver who was attempting to accumulate a continuous, sequential notation within a limited two-dimensional space. The places of “turning” in such a case would fall naturally where the phases themselves changed during the waxing and waning of the moon. Linguistically, we also refer to these as points of “turning,” and in the folk mythologies of different peoples these are recognized as points of turning in tales told about the phases of the moon. Having completed the Blanchard notation, the engraver not only had an image of the waxing and waning of the moon, but he had also created an abstracted image of the continuity and periodicity of time itself. Anyone in the culture seeing the image and knowing the tradition would probably have seen in the serpentine pattern an image of the periodicity and continuity of time, without having to “read” the individual units and sets. The number and arrangement of sets would have varied with the notation of each engraver. In the Blanchard notation, if each single mark is the abstraction of a day, and each horizontal section or phrase is the abstraction of a lunar period, the final serpentine has, in effect, become an abstraction of periodic time and process. It is significant that the image was not derived in advance as a “concept” but was probably derived from the *ad hoc*, linear sequencing process and what was apparently a traditional observation of the waxing and waning of the moon.

In much the same manner, the longer serpentine or boustrophedon notation of the Grotte du Tâi plaque, made 18,000 years later at the end of the Ice Age, can be read as an image of the “year.” The summer solstice at the right represents one point of “turning” and the winter solstice at the left represents another point of “turning”

and, in addition, the end of one year and the beginning of another. Above the Grotte du Tâi serpentine notation (Fig. 12) is a right-angle meander which, as an abstracted image, seems to say, nonlinguistically, that "we have just completed a notational sequence of which this is the abstract and we now begin another." It may be of interest that the serpentine, the spiral, and the right-angle meander, in the late Ice Age and in many post-Ice Age cultures, tended to have this nonlinguistic, kinesthetic meaning of imaging flow, process, periodicity, and continuity (Marshack, 1984a, 1985a, 1985b).

There are probably no more difficult concepts for human thought than those concerned with time and process. They are at the heart of science, philosophy, religion, and mythology. In the serpentine and the boustrophedon we have an abstraction of periodic time and process that was ultimately derived from the activity of the two-handed, vision-oriented, problem-solving capacity. These are cognized, cultural images and concepts which do not derive from language and are, in fact, not referable to language. Language, if at all, would have referred to the images. These concepts and traditions, based on observation of the processes of the sky and seasons, and on symbolic abstraction and imaging of these processes, were probably as important and adaptive as any supported by language or performed by a cutting edge.

I proceed to the tentative exploration of a still higher level of nonlinguistic, hierarchical abstraction, to concepts which were inherent and incipient in the notations but which were not necessarily apparent to the makers. In the Blanchard serpentine, the full moons fell at the left and the crescents at the right. If we stand facing south and use the period of sunset as our standard period of observation, then all the full moons will rise in the east as the sun sets in the west, all the first crescents will appear in the west as the sun sets in the west, and all the half-moons will appear high in mid-sky as the sun sets in the west. We have in the serpentine, therefore, a topographical or spatial model of the distribution of the phases. The reading is inherent in the model, but like the serpentine itself, it is an end product of the manufacturing process. Whether the topographic model was noted by the engraver, we cannot know. That it is incipient, however, indicates the nature of the nonlinguistic, vi-

sual, modeling, mapping, structuring, and abstracting potentialities being increasingly made possible by the two-handed, vision-oriented, problem-solving capacity.

If we take the Grotte du Tâi notation, we find that the same type of internal "topographic" modeling exists. If our observational standard is again sunset on the western horizon, then the movement of the sun from its low southern point on that horizon at winter solstice to its high northern point at summer solstice images the six-month swing back and forth in the Grotte du Tâi notation. The turns in the notation come at the observational points of turning on the horizon. We do not know if the analogy was noted by the engraver, but the incipience in the cultural product is significant. It is this type of reading and play that at one point began to be utilized by shamans and priests in creating cosmic symbols, mandalas, and "magic" structures and images, particularly in the post-Ice Age cultures. In these later periods, once again, these complex, cognized abstractions were not referable to or derived from language. They were products of the same abstracting and imaging capacities and processes that would later become a part of the development of science.

I am not here interested in the historical processes involved in such developments, but rather in the nonlinguistic, two-handed imaging capacity as an aspect of human neurological evolution. I am also concerned with the manner in which the processes of brain mediation function within changing and developing cultural and phenomenological contexts. For one century, archaeologists largely assigned tools and language the crucial role in hominization. In recent years, other basic biological processes have been added to those considered relevant: changing aspects of morphology such as stance, stride, hips, and teeth; changing patterns of procreation, rearing, and maturation; changing forms of bonding, sharing, and cooperation; changing types of diet; and so on. Almost all these processes, as aspects of behavior, are ultimately mediated and integrated by processes of the brain. In the examples of image, symbol, and abstraction discussed in this paper, for instance, it was neither tools nor language nor any of the patterns and processes of current biological concern that were central, though all in some measure contributed. It was the hierarchically organized mediating brain and the

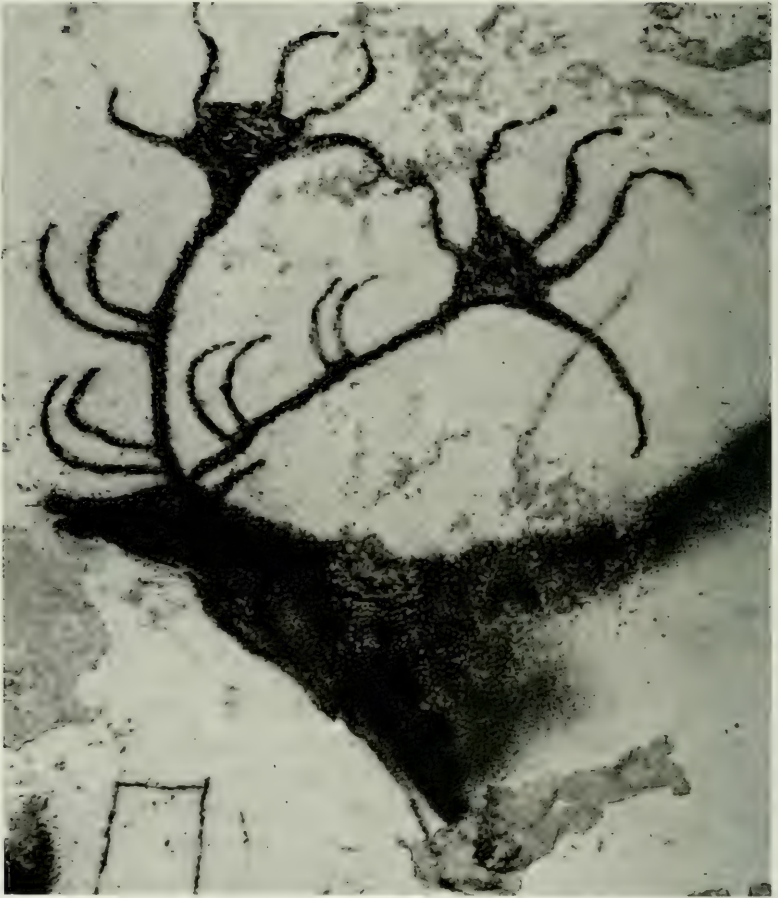


Fig. 13. Painted stag with full head of autumn antlers, head up, and mouth open baying in the autumn rut. The cave of Lascaux (photo, Vertut).

developing complexity of the capacity for problem solving, abstraction, and symboling in different vision-oriented referential modes that were crucial. I will touch on these problems again.

Let us continue our inquiry into the adaptive imaging and abstracting capacity of the Ice Age hunter with an analysis of some of the representational animal images.

In the cave of Lascaux, the best known of the French Ice Age



Fig. 14. Two bull bison from the cave of Lascaux, France. The bison at left is in summer molt, the bison at right is in full winter coat (photo, Vertut).

caves, there is the image of a stag with a full head of antlers, head up, mouth open, baying in the autumn rut (Fig. 13). This is not the image of a meal, but of the male cervid in the limited two- or three-week period of mating time. In Lascaux there is also a well-known panel of two bull bison (Fig. 14) running in opposite directions. In the half-century since the cave was discovered, no one had noted that one of the bison is in summer molt and the other has a late fall or winter coat. Each bison is also painted with a black of a different intensity and was made by a different hand. They represent different seasons, and it is possible that in the summer and fall the bison herds moved through the territory going in different directions. If we now look at the "Chinese horse" (Fig. 9), we can indicate that the horse is in its summer coat, the time when it had short hair and the cream colored underbelly was most visible. In the Ice Age winter, the wild horse grew a heavy winter coat and the demarcation of the underbelly was not as clear. Images of the horse in its heavy winter coat also appear in late Ice Age art. With these few suggestions derived from two decades of research, we can now look at some of the signs with the horse, those "barbed" signs that have been traditionally called weapons or harpoons and more recently "phallic" male symbols because they are long and thin.

In the chamber next to the hall and gallery of paintings is a room with hundreds of engravings. Some are of the type painted around the horse. Figure 15 is the kind of image that had been called a



Fig. 15. Incised image of a fern in the hall of engravings, Lascaux. The image had been called a harpoon and a phallic sign.

harpoon or phallic sign, but it is clearly a plant or fern. A set of engravings from the same hall (Fig. 16) depicts three schematic plants of exactly the type found with the "Chinese horse." For some of the images of Lascaux, we therefore have clear seasonal and sexual representations, associations, and relations. Other modes of representation and of cognized usage have been documented in other



Fig. 16. Set of incised plant forms from the hall of engravings in Lascaux, of the type found around the "Chinese horse" in a nearby chamber.

studies (Marshack, 1984b, 1985b). Here it is important to note that these images, the observations and concepts of which they were a part, and the relations among them were essentially nonlinguistic. They were recognitions derived from the vision-oriented categorizing and abstracting capacity of the left and right hemispheres, though it is likely that such other aspects of categorization as the naming

of the species and the differential details of anatomy, sex, and behavior would have been encoded in language. Language, when used within such contexts, would have been referential, marking categories and processes that were recognized and differentiated nonlinguistically and visually. Language would have served, in such use, as a contribution to what was, in essence, a *visual* form of symboling with its own syntax, modes of use and association, and vocabulary or iconography. The capacity for language and the capacity for visual symboling and problem solving are separate, highly evolved referential modalities, utilizing different areas of the brain, though the evaluation of production in either mode involves equally complex bilateral function. In addition, the making and use of these images at the right time, for the proper rituals, and in the right symbolic context would also have entailed participation of the frontal lobes with contributing input coming from subcortical centers.

The representational images of the Ice Age were all, in one way or another, "time-factored" or "time-factoring" symbols within the cultural continuum. They were highly differentiated, marked images of reference, with relevance either to the economy, to ritual and ceremonial life and mythology, or to social relations within the group. They were symbols made to be used at the right time and place for the proper purpose or to act as continuous symbols through time. Even when symbols and signs were used in personal decoration, they apparently marked sex, stage in maturation, age, status, or role specialization at any moment. As such, the many images and symbols of the Ice Age were corollary referential aspects of the more highly abstracted and specialized notations, with their implied frame of continuity and periodicity. If we examine the seasonal images in Ice Age art from Lascaux or other locations (Marshack, 1970a, 1972a, 1972b, 1975) we can theoretically place them at points on a calendar frame, either as economic, ritual, mythical, or even sacrificial species, or merely as symbols of the seasons themselves. This represents a first level of obvious, visual reference. The meanings of the animal and plant images go beyond such simple recognitions.

Each animal species depicted in Ice Age art (Marshack, 1975, p. 73) had in some degree to be hunted with a different strategy, be butchered or processed with different sets of tools, provided re-

sources or products in different ways, came from a different part of the ecology, and exhibited varied seasonal behavior. These characteristics all had to be recognized and differentiated within a successful hunting-gathering culture. It is likely that within the totally abstracted, notational sequences presented in this paper, the systematic variability of fauna and flora would have formed part of the underlying "deep structure" of the notations and their meaning. We have an interesting problem, then, one that holds also for language and writing. From the point of view of neurological function, it is obvious that the making of the notations could have been disrupted at any of a number of points, by damage to the cerebellum, to primary cortical motor areas in either the right or left hemisphere, by damage to vision or to visual association centers, by damage to orienting and spatial evaluation systems, by damage to the conceptual sequencing and "quantifying" systems of the left hemisphere, or by damage to the frontal lobe planning and motivating systems or their connections to limbic, attentional and affective systems. It is possible that a loss of the ability to name the lunar phases and periods or the seasons would have damaged the capacity to maintain the notations. Loss of the visual capacity to differentiate or categorize the animal species, their uses and behaviors, might have ended the relevance of the notations for a hunter, though the capacity to make the notations remained unimpaired. The capacity for notation was, therefore, like the capacity for language, not merely an evolved localized function, but an aspect of evolved and integrated, hierarchically organized networking processes.

These symbol systems of early modern man bring us back to Broca's finding concerning the localization of aspects of speech production in the frontal lobe of the left hemisphere and to Wernicke's subsequent finding of a specialized language comprehension area in the left temporal lobe. While the complex nature of the neurology of language is being gradually revealed, the nonlinguistic, vision-oriented capacities under discussion in this paper are probably just as complex. They are probably the result of the same trajectory of mosaic hominid neurological evolution, though the processes involved are localized in other motor and comprehension areas of the brain. Language itself, as a referential mode, apparently receives

input from visual association centers (Geschwind, 1972, 1975) and presumably also from those other categorizing, abstracting, and conceptual areas involved in the creation and use of the visual symbol systems under discussion. The underlying deep semantics of language as a referential mode rely largely on the categorizations and evaluations derived from the other sensory and associational modes. It would seem, as a result of accumulating evidence, that a proper inquiry into the human intellectual capacity requires a model of "whole-brain" function and a theory of mosaic evolution of a special type, one that deals developmentally with (1) the changing capacities of the brain for mediation in diverse modes and (2) the nature of the species-specific phenomenological and cultural "reality" that was being mediated by that expanding referential brain.

In the last few years, after analyzing the symbol systems of evolving man going back to the period of *Homo erectus* and Neanderthal man (Marshack, 1976, 1981), I have been forced to consider a model of human evolution in which toolmaking and tool use, symbol making and symbol use, and language are specialized adaptive capacities of a more generalized, hierarchically organized neurological capacity. I have suggested a mosaic model of hominid evolution in which the developing two-handed, vision-oriented competence of a bipedal hominid was a major factor in creating the conditions for reorganization of the brain (Marshack, 1976, 1984a). The model derives evolutionarily and by natural selection from capacities extant on the pongid line.

Field studies of chimpanzees in the wild have revealed that they use their hands in a wide range of tool-mediated adaptive behaviors involving different materials and strategies. Chimpanzees make and use pliable plant probes to fish for ants and termites, sticks to probe for honey, hammers of wood and stone to pound nuts. They correctly judge the weight and type of hammer needed for nuts of different hardness, they crush leaves in the mouth to make a sponge and then use their hands to sop up water from tree notches. They tear off leaves to wipe their backsides, hurl objects at intruders, noisily shake trees and branches in agonistic display, and, as hunters, they capture and rend monkeys as prey. But equally important, they use the hands affectively in hugging, grooming, begging, offering, withholding, and

in the variable range of agonistic "aggressive" displays described above. The hands are, in fact, multivalent and input to handed action comes from diverse cortical and subcortical areas of the brain. Experiments in the laboratory have revealed an even greater range in the "potential variable capacity" of the pongids for solving handed, vision-oriented problems and maintaining interpersonal relations. These capacities are neurologically and morphologically possible, but are never used in the wild.

There is an interesting aspect of this potential variable capacity as it relates to two-handed problem solving. Chimpanzees are largely ambidextrous and can also use their feet as additional, supportive sets of hands. There is a 50 percent tendency to favor one hand over the other in skilled, specifying actions. When the chimpanzee uses a tool in the wild (in ant or termite fishing, sponging, or wiping), the specifying action tends to be one-handed. When two hands are used, however, with or without tools, one hand tends to grasp or hold the object while the other performs the specifying action. As a problem becomes more complex, the tendency for one hand to perform the unfolding sequence of specifying actions, while the other performs the sequence of supporting actions, increases. This tendency is due not only to the two-handed morphology and the nature of lateralized bihemispheric mediation but also to the nature and constraints of the three-dimensional material, physical reality. It is physically impossible for the same hand to both grasp and peel a banana or perform the simultaneous actions of holding a hammer and the nut to be opened. The hands, in cooperation with the eyes, must differentially deal with these aspects of the variable, three-dimensional reality. The sensory perceptions vary for each hand as they evaluate qualities of size, shape, weight, texture, hardness, flexibility, orientation, maneuverability, and manipulability and the sequence as it proceeds and either succeeds or fails.

It is clear that these separate aspects of a complex, three-dimensional sequence cannot be simultaneously handled either by one hand or equally by two hands. The physical reality and the operation call for lateralized performance and sensory evaluation in a two-handed system, even though the sequence is mediated and evaluated by the one set of eyes. These are, nevertheless, relatively simple

aspects of two-handed problem solving. The human mode involved in the accumulation and sequencing of an abstracted notation involves a different order of neurological and referential complexity, which is comparable in its deep structure and semantics to the hierarchical organization found in language. Neurological evolution during hominization has, at one level, worked to increase the acuity and the complexity of the sensory information accruing to any one hand and the complexity of the information accruing to the visual association systems mediating each hand and the two hands jointly. These cross-modal, interhemispheric capacities and processes, while present in the chimpanzee, are not as developed as they are in man. I have suggested that selection for an increase in the neurological capacity of two-handed function would have occurred as an adjunct of increasing bipedality (Marshack, 1984a). The evolutionary problem, however, is not merely neurological and morphological. It also concerns the changing nature and the increasing complexity of the physical and material reality being dealt with or "handled" during hominization and the resulting creation of a species-specific two-handed human culture.

As the young chimpanzee matures, it learns the nature of its manipulable reality by trial and error while handling the materials of its ecology and territory. The complex skills of ant and termite fishing, probing for honey, sponging water, or breaking nuts with a hammer must be learned by example while the young chimpanzee undergoes maturation of the manipulative, coordinating, and conceptual capacities involved. These cultural skills do not occur in all chimpanzee groups and there is variation in skills between groups. Of equal importance, the skills are generalized. They are often seasonal—used only at certain times and in particular parts of the territory. Ants, termites, nuts, and honey are usually seasonal resources, and water sponging is attempted only during the dry season when the pools of water in tree notches have sunk. It is clear, then, that the potential variable capacity for problem solving and culture in the chimpanzee is only partly utilized by any one group in the wild and then only for certain temporal resources in the territory. It is important to note that none of these potential capacities and skills can be deduced from a study of chimpanzee morphology or

brain structure. It is not any particular skill but the range of the potential variable capacity for handed action that is genetic and that capacity varies with individuals within any pongid group. It is probable that in the early stages of hominization selection occurred from within the pool of genetic capacity and variability present in a pongid group.

There is another side to this problem. Some of the potential capacities of the pongid have been uncovered only in the laboratory. The so-called "proto-linguistic" capacities of pongids for use of different types of visual, hand-manipulated symbols and signs have been tested in the laboratory. What has been tested, however, is not linguistic capacity but certain aspects of the pongid vision-oriented capacity for certain forms of categorization, association, problem solving, and communication. While these capacities are involved in human language, and in the symbol systems discussed in this paper, they are at most incipient cognitive aspects of a prelinguistic capacity in the pongids, and in the tests for a supposed linguistic capacity they can function only in the constrained and artificial "cultural" contexts that are created and maintained for the pongids by humans. By contrast, true language helps to create, is derived from, and helps to maintain the cultural contexts within which it operates. There is, in fact, no human language outside of such cultural contexts. The point is crucial for understanding the difference between those extant, brain-mediated, cognitive capacities which would be incorporated into later and more evolved capacities such as language and visual imaging and symboling systems, and the nature and limitations of these early capacities. A chimpanzee can conceivably be taught to drive a tractor in constrained farming conditions set up by man, but that does not mean that it can create the culture of machinery or agriculture. We are dealing with different orders of neurological and referential capacity and function. It is this neurological and cultural difference that has not yet been investigated in proto-linguistic studies. The chimpanzee, for instance, can learn to draw circles and crosses, and perhaps even serpentines. But the capacity to use these images with the open and variable range of meanings possible to man is not possible for the chimpanzee. The chimpanzee in a man-made laboratory context can learn to gesturally

request a particular tool from another chimpanzee in order to get at an embedded or hidden food, but it cannot create or maintain the ongoing cultural contexts in which a range of tool-mediated behaviors become matters of interpersonal concern. These capacities are at most incipient, and it is from within these incipient and preparatory capacities that selection occurred.

Assuming a beginning for hominization with the bipedal, two-handed capacity that was already present in Africa in *Australopithecus afarensis*, with a brain at c. 400 cc (not much larger than the brain of the average chimpanzee) some 3.5 to 4 million years ago, I have proposed that it was from within the extant pongid "potential variable capacity" and the pool of genetic variation present for such capacity that selection for an increase in the two-handed, problem-solving capacity occurred, the capacity, therefore, for the creation of a hominoid culture (Marshack, 1984a). This is not the same as the presumed specialized capacity for making and using tools, since that is merely one aspect of the more generalized two-handed, problem-solving capacity. The selection proposed could have occurred under conditions of a slowly changing ecology or climate or more rapidly under conditions of regional crisis or stress, such as a continued period of drought or population pressure, or even periodic regional vulcanism. Under such conditions there would probably have been an initial survival advantage for those individuals within a population that were more capable of two-handed *ad hoc* problem solving, with or without tools.

The primary advantage of sustained bipedalism for an evolving protohominid in this model would have resided in the increased generalized capacity for two-handed problem solving, particularly in times of ecological crisis or periodic difficulty. As suggested elsewhere (Marshack, 1984a), the evolutionary process would initially have entailed neurological shifts or changes without necessarily requiring a major increase in brain volume. The foot, for instance, underwent major morphological change, losing much of its manipulability and sensory acuity. The hands underwent comparatively minor morphological change, i.e., the length of the thumb increased in relation to the fingers. However, there probably also occurred major neurological changes involving an increase in both the sensory

and conceptual ranges of two-handed perception, including a greater degree of hand/eye acuity and coordination in both small and large-scale handling. The process would have entailed selection for increasing the capacity for interhemispheric exchange of the hierarchical, vision-oriented, and motoric information involved in lateralized two-handed action.

Under these conditions of natural selection some groups of early hominids would have experienced an increase in the ability to “think” in terms of their changing handed capacity—to see their realm in terms of the potential opportunities it offered and the problems that could be solved in the two-handed mode, with or without tools. The increasing complexity of the physical reality being handled and thought about would have created a growing set of cultural strategies, at first not far beyond those possible for a pongid: digging for roots or tubers with a stick, probing for honey, catching and rendering small animals, scavenging large animals killed by carnivores, breaking bones for marrow, pounding nuts, probing logs or trees for grubs, carrying or cracking eggs, and manipulating plant materials or unworked stones to make a bedding site or shelter. The above activities were probably morphologically easier for a bipedal hominid than for a pongid. But a different class of activities, with or without tools, would also have been easier for a bipedal hominid: two-handed cooperation in lifting heavy logs or stones to hunt for grubs, the cooperative carrying of scavenged portions of a kill, the joint effort required for pulling down branches or shaking trees to secure fruit or nuts at the distant edges, caching stores of nuts safely under a heavy stone to be used at a later time, the cooperative hunting of small animals, the joint construction of common bedding or protective areas.

The proposed model of mosaic neurological evolution suggests that the growing suite of handed skills would have created a corollary knowledge of the seasonal variations in different parts of the territory, a lore that would be marked or “read” by visual signs in the phenomenological world but whose relevance was ultimately referable to the potentiality of the two-handed capacity and technology. A lore also would have developed of the best times of the day for different types of activity in parts of the territory. As suggested

earlier, the handed capacity has a potential that varies widely, one that functions beyond mere subsistence and food gathering. The pongid hands that are capable of agonistic or protective displays in tree and branch rattling would now probably be capable of the controlled, intentional banging together of stones, either by one individual or as a group, to create a sustained racket of terrifying protective noise. There is some indication of this potential for threatening banging, given the materials, among the chimpanzees. I am not suggesting that the strategy was used, since we do not have the evidence, but merely that the potential was present and already incipient on the pongid line. Given an ecology that supplied abundant stone resources and sources of carnivore threat in the open, the opportunities were available. The uses of banging and beating in group hunting, signaling, and music in historical human cultures provide a range of examples of the handed-acoustic capacity in diverse contexts. The potential for using the hands in interpersonal communication also exists in a range of forms on the pongid line.

It was the development of increasingly variable potential capacities, then, both as behavior and skill, rather than the capacity for any particular skill or behavior, that was the primary characteristic of human evolution. It was the increasing range of this variable potential that was to be mediated by the larger, more complex brain. The model suggests that vocalization, or language, in this sense, probably evolved as a *variable* marking capacity in the acoustic mode, comparable neurologically to the potential capacities of the two hands. Current theories concerning the adaptive value of the two-handed bipedal mode, which suggest use of the freed hands for carrying infants or the portage of food to a home site, deal only with certain specialized functional aspects of the developing potential, rather than with the more generalized processes suggested here. Other vertebrates carry infants and bring food back to a home base. The hominids probably began to use their hands in a wide range of interpersonal activities because the hands were now available as more efficient, generalized problem solvers in the new and more variable bipedal context.

The mosaic evolutionary model suggests that it was probably during or just after the adaptive success of the developing two-handed,

vision-mediated capacity had been established that the benefits of an increase in brain volume and neurological capacity would have become apparent, not merely for the sensory and motor skills involved in real-time handed actions and sequences, but for that more important adjunct set of cortical and subcortical capacities that makes the two-handed system in man important in the periodic and variable practical and symbolic programs of culture. These include the many capacities involved in the maintenance of social patterns and interactions and in the evolution of language. Aspects of these capacities have been touched on in our analysis of the Ice Age artifacts. Selection for an increase in these capacities would have occurred at many points in the biological and social process.

It could have occurred at the population level, the advantage of a more efficient two-handed capacity probably being most apparent to a group of hominoid bipeds that found itself in a more difficult or complex ecology (Marshack, 1984a). At another level, the increase in capacity could have occurred by alterations in the rate of fetal development of certain subsystems of the brain, or in changes in the rates of maturation and experiential encoding for different skills. Above all, selection could have occurred at the adult level, screening for those most capable of functioning in an increasingly complex practical and symbolic culture.

Because the two-handed mode was part of a complex, lateralized neurological cognitive system, a generalized system that would serve language as well, the neurological changes that were entrained in hominization would have involved the full set of whole-brain cortical and subcortical capacities. Such capabilities are manifested as selective attention and observation, categorizing, abstraction, imaging, modeling, mapping, planning, creating rules and programs, motivating, coordinating, sequencing, and the still higher capacities for evaluating objects, plans, and actions. These are the generalized capacities that make the specialized skills of the hands and language variable, adaptive, and human. The presence of each of these capacities is apparent in the Ice Age symbol systems. They are among the hierarchically organized capacities that Alexander Luria, the Soviet neuropsychologist, had suggested were involved in the "integration of higher cortical function." These cognitive capacities are

neither "handed" nor "linguistic." However, they provide the deep semantic structure that makes the range of handed and linguistic skills found in man both human and cultural.

This paper began with the nonlinguistic, two-handed, vision-oriented capacity evident in certain artifacts of early man. The mosaic evolutionary model I am proposing suggests that language, as a *referential* mode, would have become increasingly adaptive as a consequence of the general neurological and cultural changes being instituted within a particular group of hominids in an increasingly complex ecological, social context. The model therefore suggests that language would not have been equally adaptive or under equally strong selective pressure for all bipedal hominoids. Those hominoids who became specialized plant feeders in less complex, more stable, and less difficult or variable ecologies, such as the later gracile and robust australopithecines, would not have needed language at the same level of referential capacity. Nor would they have needed a two-handed capacity, and tools or other forms of vision-mediated referential systems at the same level of complexity.

Whole-brain cortical and subcortical function cannot be read from the surface architecture of the brain. Contemporary studies of hominid and hominoid endocasts cannot provide more than a gross indication of those changes occurring in cortical surface morphology that would suggest functional changes in the capacity of handed, vision-oriented problem solving or language. Endocranial studies of the skulls of early man do document the major increase in brain volume, enlargement of the temporal, parietal, and frontal areas, and certain more subtle changes such as a developing asymmetry of the left occipital and a right frontal petalia. Such endocast studies cannot, however, verify with certainty enlargement of Broca's area for speech production in the early hominid skulls. Holloway (1981, 1983) has estimated that the areas of the cortex most likely to have undergone extensive morphological change and enlargement from pongid to human are the parietal lobe, areas of the occipital visual system, and the middle dorsofrontal area. These areas are part of the network that would have been crucial for the development of the hominid visual capacity for symboling and would have supplied some of the referential semantic "deep structure" to language. The

occipitoparietal association area involves the *angular gyrus* which Geschwind (1964, 1972) has suggested is a crucial cross-modal association area for language. It has connections both to Wernicke's area which it adjoins and to Broca's area and the motor areas of the face, by the pathway of the *arcuate fasciculus*. There may also be connections from the *angular gyrus* via the *arcuate fasciculus* to higher vision-oriented association areas of the handed capacity. Geschwind (1967) wrote that "carrying out a task under visual control . . . probably involves a pathway running from [left hemisphere] visual association cortex to motor association cortex and therefore makes use of fibers which also run in the *arcuate fasciculus*." These diverse suggestions, together with the proposed evolutionary model derived from an analysis of the symbolic materials of early man, suggest that development of the lateralized two-handed capacity had become, at some point in the process of hominization, a corollary aspect of the separate development of language in the vocal/auditory mode.

The first clear evidence we have of substantial brain enlargement and of enlargement of major association areas, probably including Broca's and Wernicke's areas, occurred during the stage of *Homo habilis*, around 2 to 2.5 million years ago, together with the first evidence of hammered and chipped pebble tools. By the next stage, a half million or a million years later, in *Homo erectus*, both brain volume and the specialized areas of higher cortical function are greatly enlarged and we have evidence of a more advanced, visually mediated, shaped, and chipped stone tool kit. There is a suggestion of a more complex two-handed culture and therefore a more complex referential need. The mosaic evolutionary model being proposed, however, suggests that it was neither the tool kit nor language, separately or together, that was the central adaptive mechanism in this developing capacity. Rather, it was the hierarchically organized "whole brain function" which was capable of mediating and coordinating the range of potentially variable cultural and practical uses available to these two sensorily and morphologically separate, but ultimately vision-mediated, modalities. The model also suggests, by references to the evidence of complex pongid cultural behavior in the wild and in the laboratory, that selection operated on these

cognitive capacities. These aspects of potentially adaptive neurological function in the pongid cannot be derived from the morphology of the skeleton or the brain. None of the chimpanzee's suite of "cultural" behaviors noted in the wild can, for instance, become archaeological. It is only late in hominid evolution that certain aspects of stone-tool-mediated behaviors become artifactual.

Language, in this model of evolving capacity, can be considered a developing referential function in the acoustic/vocal mode, which became increasingly capable of marking the potentially variable cultural and social milieu, much as stone tools can be considered as functional adjuncts of the two hands in solving a range of problems in the potentially variable material and physical realm. It is at the juncture of these two evolving capacities that we come, neurologically, to those nonlinguistic, visual symboling systems that at some point in hominid evolution become artifactual and with which we began our discussion. These late systems represent modes of problem solving, of reference, and of marking certain aspects of the relevant cultural reality by use of the two-handed capacity and a two-handed technology.

The first archaeological evidence for the manufacture and symbolic use of red ochre, and the possible contemporary symbolic alteration and use of human skulls, appears late in the *Homo erectus* period, c. 400,000–250,000 B.C. *Erectus* was at this stage already on the way to becoming *Homo sapiens*. The mosaic model of a developing potential capacity suggests that these were probably not the first symboling efforts—that they were end products of two-handed capacity and use. The sparse archaeological evidence for the use of ochre and human skulls suggests that these artifacts represent traditions rather than first inventions. Again, the model suggests that such symboling efforts were not intended to serve a particular adaptive, cultural purpose but a potentially variable range of referential and marking purposes. The uses of red ochre, for instance, would probably have varied between groups and within groups. The model suggests that the symboling capacity as a function of brain mediation, expressed through uses of the hands and uses of early language, would have been open and variable. That increasing variability of function would have been made possible by the developing network of cross-

modal, associational, and increasingly lateralized processes being hierarchically organized and integrated in the hominid brain.

The model suggests some of the difficulties encountered in establishing the pongid capacity for using "proto-language" and symbols or for making images of "art" in artificial contexts. In these instances one is testing those aspects of pongid capacity that were incipient and, at most, extant, but were still neurologically insufficient for creating and maintaining the range of abstracted referential uses found in human art and language. The point is crucial for understanding what it was that evolved on the human line and for our understanding of late modern uses of both art and language.

Communication among other species, whether in the visual, acoustic, or chemical mode, almost always constitutes a form of "real" or present-time marking of a constrained, intraspecific relationship or context. The informational, signaling content of such communication can refer to aspects of seasonal sexual behavior; it can involve alarm calls, territorial marking, display behavior, neonate imprinting, and mother-infant interaction; it can facilitate cooperative group hunting or protective activities; it can even involve such examples as the nonvertebrate communication found in bee "language," which provides orienting information about foods available at one point and one moment in the territory. One can add to these "real-time" communications the catalog of primate gestures and vocalizations or the bird song of the male in territorial and sexual behavior during the breeding season. Because of the constrained, intraspecific and context-bound nature of such signaling modes (specific to age, sex, season, and species), they can be largely genetically encoded and experientially and maturationally released.

Human language, however, even at the simplest and most basic level, as evidenced in a child's acquisition of language, marks and differentiates the inherently variable and developmentally changing phenomenological and social reality. From its first words, the child deals with the marked aspects of a variable human culture. Even when a child's language deals with simple ego desires, these develop and change as the child matures within the cultural context. The reason is that human language involves an experiential, maturing neurology that refers developmentally to a changing hierarchically

organized cultural reality. In this it differs from context-bound signaling. It is the neurology of this “open-ended” and variable referential capacity, as it is expressed at the mature, adult level, that interests me in this paper. This interest extends to the neurology of those general cognitive, conceptual, and problem-solving capacities that are involved in the visual symbol systems of the Ice Age and were presumably also involved in language.

This neurology involves the capacity for differentiating and categorizing objects, species, and processes and for the internalized abstracting of forms and processes; it includes the capacity for conceptual mapping and modeling and for planning and performing complex sequences of action and evaluating such unfolding sequences. These are all present at the primate or pongid level, but with a less evolved neurological capacity. I have suggested (Marshack, 1984a) that it was the developing two-handed neurology that helped in the creation of a more complex referential, vision-oriented body of nonlinguistic, functional knowledge and culture, one that would have served the deep semantic structure of language, just as the lateralized two-handed neurology may have served as a conjunctive model for the developing lateralized language capacity. There may be a possibility of verification or clarification of this model in comparative functional and behavioral experiments with primates and humans.

If we now return to our limestone shelf on the cliff overlooking Les Eyzies and look across that valley in evolutionary perspective, we can probably assume that a population of late *Homo erectus*, c. 300,000 B.C., or of Neanderthals of 100,000–40,000 B.C., or of modern Cro-Magnons, would all have seen the same periodic patterns of the sky and seasons with their accompanying changes in flora and fauna, if they lived on that shelf. Climates varied through this period of shifting Ice Ages, but the essential temperate zone periodicities of the seasons and of nature at that latitude in Europe would have persisted. The mosaic evolutionary model suggests that the different types of humans inhabiting that shelf would have “seen” a different relevant practical and marked or symbolic reality. The differences would have been partly due to biology—differences in evolved levels

of neurological capacity among *Homo erectus* and the later *Homo sapiens neanderthalis* and Cro-Magnon, or *Homo sapiens sapiens*; and it would have been partly due to the uses that were possible in two-handed problem solving and an accompanying technology; and partly due to the level of symbolic marking present or possible in each period, whether in speech or in visual modes.

Each group of humans would have noted the sources of raw materials, whether of stones for tools, wood for fire, skins for clothing, meat for eating, colors for symbolic purposes, and so on. However, the social and cultural complexity—the breakdown of that valley and its surround conceptually into areas and periods of specialized seasonal activities and the symbolic and linguistic marking of these abstracted categories of relevance—would have differed. I assume that our Cro-Magnon hunter, after he had lived in that valley for a number of generations, saw it as a structured, dynamic, and patterned whole: he recognized it in terms of the specialized uses possible in different parts of the territory in different seasons. There were probably symbolic zones or areas that were taboo or sacred, such as areas of burial, caves for ritual, or places of a recently remembered tragedy. He could probably locate from that shelf a particular source of red ochre. There may even have been a contact territory up or down river beyond his own territory for obtaining symbolic items, perhaps even by exchange. He had a far more complex set of associations than his Neanderthal or *erectus* predecessors had. Red ochre, for instance, was not only a potential source for decorating his tools, his symbolic artifacts, and himself. It also could be used for decorating his shelter, in burials, in cave painting, in curing ceremonies, and perhaps in preparing skins. It had an increased range of potential variability. It was a material that could be used in times of crisis such as death and curing or in times of celebration and seasonal ritual. The famous early Cro-Magnon figurine, the “Venus of Willendorf,” was heavily covered with red ochre and may have been periodically renewed by overpainting.

There were also other specialized activities that would have been related to the conceptual cognitive map and network of reference maintained by the brain. Our Cro-Magnon notation keeper would have seen the valley and its round of processes in terms of his own

specialized role as keeper of time and the schedule of cultural activities. As a tool maker and tool user he would have been aware of the periodic availability of antlers for making tools and carvings at the river crossing for reindeer below him. He would have been aware of the relation of the position of the early spring setting sun to the spring run of salmon in the river and of the possible relevance of these two events to an aggregation of relatives or neighbors for a feast of the first run. He may have had a name for the sun and moon and a mythological explanation for the processes he observed and the rituals relating to them. Standing on that shelf, he would have known in which direction threats lay, whether from humans or from seasonal storms that arrived with winds from different directions. He could probably read his sky to judge the weather of that day and make his decisions. In every instance, the meaning and relevance of these observations would have been ultimately related to the two-handed competence and the symbolic capacity for differentiating and marking the relevant categories and processes involved. Together these made up the neurologically mediated contents of what we would call his "culture." The potential complexity of this referential realm would have differentiated his culture from that of earlier men who may have stood on that same shelf.

It is more than a century since Lartet and Broca made their pioneering inquiries into early man and the brain. In that century the archaeologists of early man have constructed a rough outline of the time scale and the morphological changes involved in hominization. These have largely validated the original scenario suggested by Darwin. Darwin, however, in the 19th century, could only deal with the more obvious and gross aspects of behavior and morphology. He could not approach the core problem of a changing neurology and potential capacity. Relevant to this problem is the 20th-century archaeological finding that there were at least two diverging lines of bipedal hominoids, evidenced by skeletal and dental differences and a different diet. Different adaptive modes entail different types and levels of neurological mediation. To date, little discussion has been directed to the nature of the neurological differences and capacities that must have accompanied these different hominoid and hominid

adaptations. It is to some aspects of this problem that I have directed attention.

Investigations of primate and human brains have progressed far beyond what Darwin could have conceived. These studies have differentiated many levels of specialized neurological function; they have distinguished dysfunction or abnormality caused by localized damage or surgical disconnection from that caused by genetic factors; they have been able to image certain real-time aspects of whole brain function by tomography or evoked potentials; and they have succeeded in the reductive analysis of single neurons and of synapse function between them. Functional asymmetry in right and left hemispheres and the differences between male and female capacity and neurology are under investigation. However, few of these studies have considered the *evolution* of hierarchically organized "whole brain function" or the relation of the changing brain as a mediating organ to an increasingly complex physical and cultural realm.

Alexander Luria (d. 1977) made a major effort in this direction by his studies of damaged brains. He was largely motivated in his original research by the "Marxist" effort of the pioneering Soviet psychologist L. S. Vygotsky (1962, 1978) to create a theory of the role of the brain, language, imaging, and handed competence or technology in history and culture. Luria eventually attempted to present a unified picture of the adult cultural brain in his *Higher Cortical Function of the Brain* (1966) and his earlier, more tentative volume on psychological modes of thinking in different cultures, *Cognitive Development and Its Cultural and Social Functions* (1976). It was apparently because of this background and his interest in the cultural brain that Luria found the research and inquiry briefly presented in this paper personally relevant. When we met, toward the end of his life, he praised the direction of the inquiry. He recognized that his effort to explain the cultural brain had only partially succeeded. He had only barely touched on the many influences of the subcortical brain and the limbic system on higher cortical function and his major work predated research with split brains and its insight into disassociation of function. Above all, when we met, he stressed the inadequacy of a too simple "Marxism" (Kotchetskova, 1978) in

its attempt to explain the evolution of the brain in utilitarian, materialistic terms related to "labor." Such an approach left out symboling, language, and conceptual thinking. He looked to the new research then under way in neurology to probe more deeply into the role of the subcortical brain and limbic system. He was particularly interested in research that would explore the evolution of "higher cortical function" as the essential mediator and maintainer of culture and as a crucial aspect of and participator in human history and change. He suggested that the fundamental questions I had been asking were of the same type that Vygotsky and he had been exploring from a different direction.

The broad questions, then, concerning man, his brain, and his evolution, which were in different ways of interest to Darwin, Lartet, Broca, and Luria, still remain to be answered. They have been approached from a specialized point of view and with a particular set of data in the present inquiry.

* * *

This paper is dedicated to Norman Geschwind, friend and colleague, who died November 5, 1984, the day on which this manuscript was completed. Geschwind, reading my book (Marshack, 1972a), asked me to present the annual lecture of the Boston Neurological Society in 1974. In the decade that followed he was a consistent supporter of the research and inquiry. As a neurologist interested in the "cultural" brain, he has contributed profoundly to the deepening inquiry. Geschwind presented the James Arthur Lecture in 1980.

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**Out of print.

†Published version: *The Brain in Hominid Evolution*, New York: Columbia University Press, 1971.

JAMES ARTHUR
1842-1930

Born in Ireland and brought up in Glasgow, Scotland, James Arthur came to New York in 1871. Trained in mechanics and gear-cutting, he pursued a career in the manufacture and repair of machinery, during the course of which he founded a number of successful businesses and received patents on a variety of mechanical devices. His mechanical interests evolved early into a lifelong passion for horology, the science of measuring time, and he both made some remarkable clocks and assembled an important collection of old and rare timepieces.

Early in this century James Arthur became associated with the American Museum of Natural History, and began to expand his interest in time to evolutionary time, and his interest in mechanisms to that most precise and delicate mechanism of them all, the human brain. The ultimate expression of his fascination with evolution and the brain was James Arthur's bequest to the American Museum permitting the establishment of the James Arthur Lectures on the Evolution of the Human Brain. The first James Arthur Lecture was delivered on March 15, 1932, two years after Mr. Arthur's death, and the series has since continued annually, without interruption.

THE USES OF CONSCIOUSNESS

As is customary on occasions such as this, I should start by thanking my hosts for the surprising gamble they have taken in asking me to give this lecture. The James Arthur Lecture on the Evolution of the Human Brain has brought to this museum a series of distinguished scientists who, in the laboratory or field, have made important discoveries about the workings of the human brain or about human evolution. I have done neither. I hope, therefore, that you will not be too surprised when I tell you that in my lecture this evening I shall have no new research findings to report. In truth I shall have rather little to say about the facts of evolution, and even less to say about the detailed workings of the brain.

I am going to be talking about consciousness—about what consciousness is, and about what part it plays in the natural history of human beings. I shall try to give scientific answers to both questions. But they will, I should say, be “armchair answers”: based not so much on new experiments or novel facts, as on a reassessment of facts that we already know. Armchair theorizing has frequently been castigated as too easy. “Unfortunately,” Diderot wrote in 1754, “it is easier and quicker to consult oneself than to consult nature.”¹ I take his point. But consulting nature on the subject of consciousness is not, I’m afraid, something that anyone that I know is able to do. And since it so happens that one of the few sure facts about consciousness is that every one of us has experienced it in his or her own person, to consult oneself may not be such a bad plan after all.

But that’s where *I* must take a gamble. When I talk about consciousness, I’m talking about inner experience—about what it *feels* like to be oneself, to have sensations, thoughts, moods, desires, subjective reasons for one’s actions. And if you are to understand—or even be interested—in what I am going to say, I have to assume that we have some sort of shared reference point. But do we? Consciousness is a notoriously tricky concept. No one ever taught us how to use the word correctly. When we were small and learning language, no one ever pointed out an example of consciousness and said, “That’s consciousness; remember that next time you see it”—in the way they might have pointed out other things in our envi-

ronment and said, “That’s a rabbit . . . or a Spring day . . . or a map of New York.” If I and you *do* use the word in the same way, we do not have our nursemaids to thank for it. Perhaps we should thank Mother Nature—well, we shall see.

When I was asked for a title for the lecture, I suggested “The Uses of Consciousness.” But, now that it comes to it, I realize I am going to spend a fair bit of time on prior issues—what consciousness is good for as a *concept*, before I get to the question of what it’s good for *in our lives*.

A lecture should have a hero. I give you Denis Diderot—the 18th century French philosopher, novelist, aesthete, social historian, political theorist, and editor of the *Encyclopaedia*. It’s hard to see how he had time but, alongside everything else, Diderot wrote a treatise called the *Elements of Physiology*—a patchwork of thoughts about animal and human nature, embryology, psychology, and evolution. And tucked into the *Elements of Physiology* is this remark:

If the union of a soul to a machine is impossible, let someone prove it to me.
If it is possible, let someone tell me what would be the effects of this union.²

Now, replace the word “soul” with “consciousness,” and Diderot’s two thought-questions become what are still the central issues in the science of mind. Could a *machine* be conscious? If it were conscious, what *difference* would it make? I shall—if you’ll allow me—use the term “soul” and the more modern terms “consciousness” or “self-awareness” more or less interchangeably throughout this talk, without (I hope) misrepresenting anyone or anything. That granted, I have in Diderot’s two questions the framework for everything I want to say.

The context for those questions is not hard to guess. Diderot was simultaneously appalled and fascinated by the dualistic philosophy of René Descartes. Diderot wrote:

A tolerably clever man began his book with these words: “*Man, like all animals, is composed of two distinct substances, the soul and the body.*”

I nearly shut the book. O! ridiculous writer, if I once admit these two distinct substances, you have nothing more to teach me. For you do not know what it is that you call soul, less still how they are united, nor how they act reciprocally on one another.³

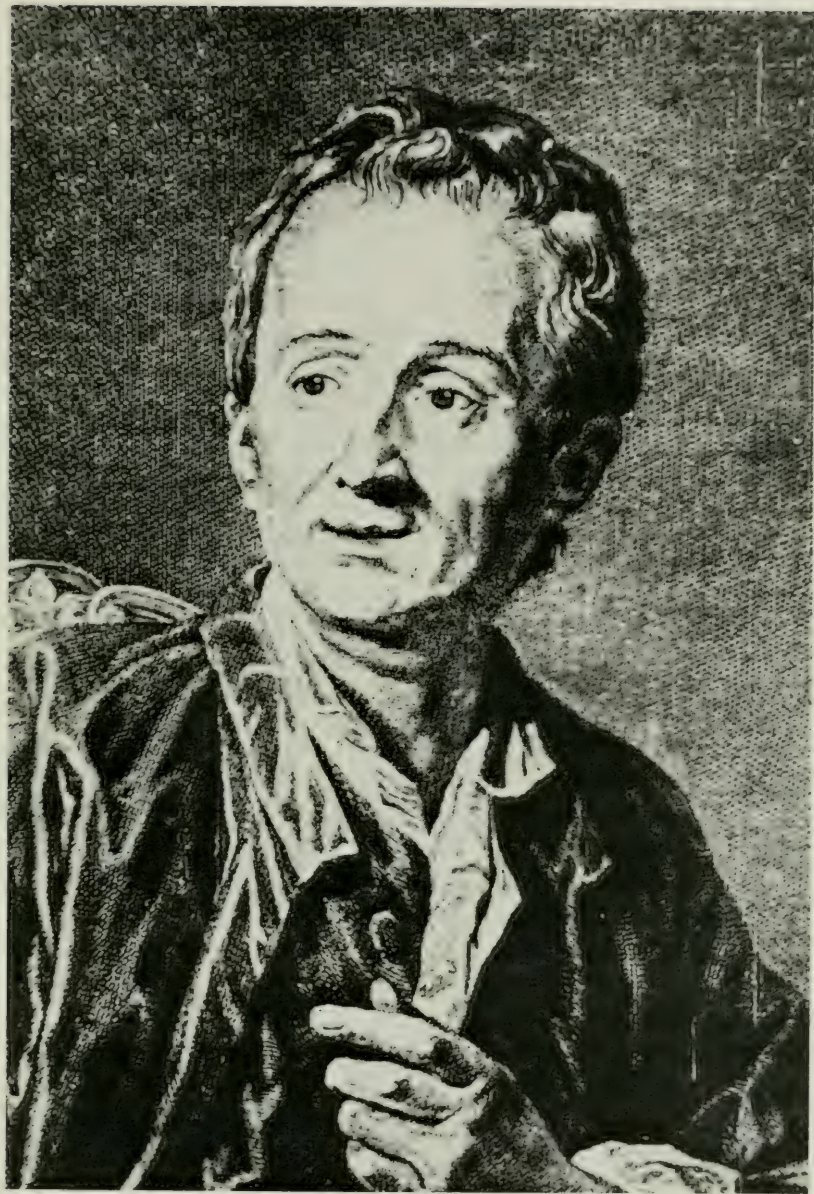


Fig. 1. Denis Diderot, 1713–84.

Ridiculous it may have been. But sixty years later, the young Charles Darwin was still caught up with the idea: "The soul," he wrote in one of his early notebooks, "by the consent of all is super-added."⁴

This is one issue that the philosophy of mind has now done something to resolve. First has come the realization that there is no need to believe that consciousness is, in fact, something distinct from the activity of the physical brain. Rather, consciousness should be regarded as a "surface feature" of the brain, an emergent property that arises out of the combined action of its parts. Second—and in some ways equally important—has come the realization that the human brain itself *is* a machine. So the question now is not, "*Could* a machine be conscious or have a soul?" Clearly it could: I am such a machine, and so are you. Rather, the question is, "What *kind* of machine could be conscious?" How much more and how much less would a conscious machine have to resemble the human brain—nerve cells, chemicals, and all? The dispute has become one between those who argue that it's simply a matter of having the appropriate "computer programs," and those who say it's a matter of the "hardware," too.

The philosopher Dan Dennett, for example, is all for programs. There cannot be anything, Dennett maintains, so especially special about nerve cells. If a human brain can carry out the logical functions that, when translated into behavior, persuade us that it's conscious, then so too—at least in theory—could an artificial brain. I say "persuade us that it's conscious" because that—in Dennett's view—is precisely what human brains do: we don't *know* that any other human being is conscious; we are simply led to believe that they are by their behavior.⁵ I need hardly tell you that not everyone accepts this way of looking at things. John Searle, for example, finds the idea of artificial consciousness deeply troubling. For him, there is a fundamental distinction to be drawn between a human who is "genuinely" conscious, and a machine which merely behaves "as if" it were conscious.⁶ But this is just the distinction that Dennett says is philosophically no good. And so the argument goes on—at the level, so far as I can read it, of "'Tis . . . 'Tisn't."

This is not a dispute on which I want to dwell, partly because I'm not sure that it will ever be resolved, but chiefly because it seems

to me to jump the gun. It is all very well to discuss whether a machine which fulfills in every respect our *expectations* of how a conscious being *ought* to behave would actually be conscious. But what exactly are our expectations, and how might we account for them? In short, what do we think consciousness *produces*? It brings me directly to Diderot's second question. "If a machine could be united to a soul, what effects—if any—would it have?"

When Diderot asked it, my guess is he was asking rhetorically for the answer, "*None*." A machine, he was prepared to imagine, might have a soul—and yet for all practical purposes it would surely be indistinguishable from a machine without one:

What difference between a sensitive and living pocket watch and a watch of gold, of iron, of silver and of copper? If a soul were joined to the latter, what would it produce therein?⁷

Presumably, as a time-keeper—and that, after all, is what a watch does best—the watch would be just the same watch it was before: the soul would be no *use* to it, it wouldn't *show*.

I do not want to pin onto Diderot the authorship of the idea of the functional impotence of souls. But whenever it came, and whether or not Diderot got there, the realization that *human* consciousness itself might actually be useless was something of a breakthrough. I remember my own surprise and pleasure with this "naughty" idea, when I first came across it in the writings of the Behaviorist psychologists. There was J. B. Watson, in 1928, arguing that the science of psychology need make no reference to consciousness:

The behaviorist sweeps aside all medieval conceptions. He drops from his scientific vocabulary all subjective terms such as sensation, perception, image, desire, and even thinking and emotion.⁸

And there, as philosophical backup, was Wittgenstein, arguing that concepts referring to internal states of mind have no place in the "language game."⁹ If nothing else, it was an idea to tease one's school-friends with. "How do I know that what I experience as the colour red, isn't what you experience as green? . . . How do I know that you experience anything at all? You might be an unconscious zombie." But I called it a naughty idea, and it is an idea which has had a good run, and now can surely be dismissed.

I will give two reasons for dismissing it. One is a kind of Panglossian argument, to the effect that whatever exists as a consequence of evolution must have a function. The other is simply an appeal to common sense. But before I give either, let me say what I am *not* dismissing: I am not dismissing the idea that consciousness is a second-order and in some ways inessential process. I freely admit that in certain respects the behaviorists may have been right.

Diderot gives a nice example of *unconscious* behavior:

A musician is at the harpsichord; he is chatting with his neighbour, he forgets that he is playing a piece of concerted music with others; however, his eyes, his ear, his fingers are not the less in accord with them because of it; not a false note, not a misplaced harmony, not a rest forgotten, not the least fault in time, taste or measure. Now, the conversation ceases, our musician returns to his part, loses his head and does not know where he has got to. If the distraction of the conscious man had continued for a few more minutes, the unconscious animal in him would have played the piece to the end without his having been aware of it.¹⁰

So the musician, if Diderot is right, sees without being aware of seeing, hears without being aware of hearing. Experimental psychologists have studied similar examples under controlled laboratory conditions and confirmed that the phenomenon is just as Diderot described: while consciousness takes off in one direction, behavior may sometimes go in quite another. Indeed consciousness may be absent altogether. A sleep-walker, for example, may carry out elaborate actions and even hold a simple conversation without waking up. Stranger things still can happen after brain injury. A person with damage to the visual cortex may lack all visual sensation, be consciously quite blind, and none the less be capable of “guessing” what he would be seeing *if* he could see.¹¹ I have met such a person: a young man who maintained that he could see nothing at all to the left of his nose, and yet could drive a car through busy traffic without knowing how he did it.

So, that is what I am *not* dismissing: the possibility that the brain can carry on at least part of its job without consciousness being present. But what I *am* dismissing is the possibility that when consciousness *is* present it isn’t making any difference. And let me now give the two reasons.

First the evolutionary one. When Diderot posed his question, he

knew nothing about *Darwinian* evolution. He believed in evolution, all right—evolution of the most radical kind:

The plant kingdom might well be and have been the first source of the animal kingdom, and have had its own source in the mineral kingdom; and the latter have originated from universal heterogeneous matter.¹²

What is more, Diderot had his own theory of selection, based on the idea of “contradiction”:

Contradictory beings are those whose organization does not conform to the rest of the universe. Blind nature, which produces them, exterminates them; she lets only those exist which can co-exist tolerably with the general order.¹³

Surprising stuff, seeing as it was written in the late 18th century. But note that, compared to the theory Darwin came up with 80 years later, there is something missing. Diderot’s is a theory of *extinction*. According to him, the condition for a biological trait surviving is just that it should not contradict the general order, that it should not get in the way. Darwin’s theory, on the other hand, is a theory of adaptation. According to him, the condition for something’s surviving *and spreading through the population* is much stricter: it is not enough that the trait should simply be noncontradictory or neutral; it must—if it is to become in any way a general trait—be positively beneficial in promoting reproduction.

This may seem a small difference of emphasis, but it is crucial. For it means that when Diderot asks—of consciousness or anything else in nature—“What difference does it make?” he can reasonably answer, “None.” But when a modern Darwinian biologist asks it, he cannot. The Darwinian’s answer has to be that it has evolved because, and only because, it is serving some kind of useful biological function.

Then, either we throw away the idea that consciousness evolved by Darwinian natural selection, or else we have to find a function for it. We can, of course, throw it away. Perhaps Darwin himself did: he was, as I mentioned, prepared to imagine that consciousness has been in some way “super-added”—presumably by some non-natural process. But that is no reason why we should go along with him. I assume—I hope I’m right in this—that everyone present here

is a Darwinian, and that you, like me, would *like* to find a function for consciousness.

You may wonder, however: can we still expect consciousness to have a function even if we go along with the idea that it is in fact a “mere surface feature” of the brain? Well, let’s not be misled by the word “mere.” We might say that the colors of a peacock’s tail were a mere surface feature of the pigments, or that the insulating properties of fur were a mere surface feature of a hairy skin. But it is, of course, precisely on such surface features that natural selection acts: it is the color or the warmth that matters to the animal’s survival or reproductive success. Philosophers have sometimes drawn a parallel between consciousness as a surface feature of the brain and wetness as a surface feature of water. Suppose we found an animal made entirely out of water. Its *wetness* would surely be the first thing for which an evolutionary biologist would seek to find a function.

Nonetheless, we do clearly have a problem—and that is to escape from a definition of consciousness that renders it self-evidently useless and irrelevant. Here the philosophy of mind has, I think, been less than helpful. Too often we have been offered definitions of consciousness that effectively hamstring the inquiry before it has begun: for example, that consciousness consists in private states of mind of which the subject alone is aware, which can neither be confirmed nor contradicted, and so on. Wittgenstein’s words, at the end of his *Tractatus*, have haunted philosophical discussion: “Whereof we cannot speak, thereof we must be silent.”

All I can say is that neither biologically nor psychologically does that feel right. Such definitions, at their limit (and they are meant, of course, to impose limits), would suggest that statements about consciousness can have no *information content*—technically that they can do nothing to reduce anyone’s uncertainty about what’s going on. I find that counterintuitive and wholly unconvincing. Which brings me to my second reason for dismissing the idea that consciousness is of no use to human beings, which is that it is contrary to common sense.

Suppose I am a dentist, and am uncertain whether the patient in the chair is feeling pain. I ask him, “Does it hurt?” and he says, “Yes . . . I’m not the kind of guy to show it, but it does *feel* awful.”

Am I to believe that such an answer—as a description of a conscious state—contains *no* information? Common sense tells me that when a person describes his state of mind, either to me or to himself (not something he need be able to do, but something which as a matter of fact he often can do), he is making a revealing self-report. If he says, for example, “I’m in pain,” or “I’m in love,” or “I’m having a green sensation,” or “I’m looking forward to my supper,” I reckon that I actually know more about him; but more important, that *through being conscious* he knows more about himself.

Still, the question remains: what sort of information is this? What is it about? And the difficulty seems to be that whatever it *is* about, at least in the first place, is private and subjective—something going on inside the subject which no one else can have direct access to. I think that this difficulty has been greatly overplayed. There is, I’d suggest, an obvious answer to the question of what conscious descriptions are about, namely that they are descriptions of what is happening inside the subject’s *brain*. For sure, such information is “private”—but it is private for the good reason that it happens to be *his* brain, hidden within his skull, and that he is naturally in a position to observe it, which the rest of us are not. Privacy is no doubt an issue of great biological and social significance, but I don’t see that it is philosophically all that remarkable.

My suggestion that consciousness is a “description of the brain” may nonetheless seem rather odd. Suppose someone says, for example, “I’m not feeling myself today.” That certainly doesn’t sound like a description of a brain state. I agree. Of course it doesn’t *sound* like one, and no doubt I’d have trouble in persuading most people that it was so. Few people, if any, naturally make any connection between mind states and brain states. For one thing, almost no one except a brain scientist is likely to be interested in brains as such (and most people in the world probably don’t even know they’ve got a brain). For another, there is clearly a huge gulf between brain states, as they are in fact described by brain scientists, and mind states as described by conscious human beings, a gulf which is practically—and, some would argue, logically—unbridgeable.

Yet is that really such a problem? Surely we are used to the idea that there can be completely different ways of describing the same

thing. Light, for example, can be described either as particles *or* as waves, water can be described either as an aggregation of H₂O molecules *or* as a wet fluid, Ronald Reagan can be described either as an aging movie-actor *or* as the President of the United States. The particular description we come up with depends on what measuring techniques we use and what our interests are. In that case, why should not the activity of the brain be described either as the electrical activity of nerve cells *or* as a conscious state of mind, depending on who's doing the describing? One thing is certain: that brain scientists have different *techniques* and different *interests* from ordinary human beings.

I admit, however, that I am guilty of some sleight of hand here. It is all very well to suggest that consciousness is "a description" of the brain's activity by a subject with appropriate techniques and interests; but what I have failed to do is to locate this conscious subject anywhere. "To describe" is a transitive verb. It requires a subject as well as an object, and they cannot, in principle, be one and the same entity. A brain, surely, cannot describe its own activity, any more than a bucket of water can describe itself as wet. In the case of the water, it takes an observer outside the bucket to recognize the water's wetness, and to do so he has to employ certain observational procedures: he has to stick his hand into it, swish it around, watch how it flows. Who, then, is the observer of the brain?

Oh dear. Am I stuck with an infinite regress? Do I need to postulate another brain to describe the first one, and then another brain to describe that? Diderot would have laughed:

If nature offers us a difficult knot to unravel, do not let us introduce in order to unravel it the hand of a being who then becomes an even more difficult knot to untie than the first one. Ask an Indian why the world stays suspended in space, and he will tell you that it is carried on the back of an elephant . . . and the elephant on a tortoise. And what supports the tortoise? . . . Confess your ignorance and spare me your elephant and your tortoise.¹⁴

You can hardly expect me, halfway through this lecture, to confess my ignorance. And in fact I shall do just the opposite. The problem of self-observation producing an infinite regress is, I think, phony. No one would say that a person cannot use his own eyes to observe his own feet. No one would say, moreover, he cannot use his own

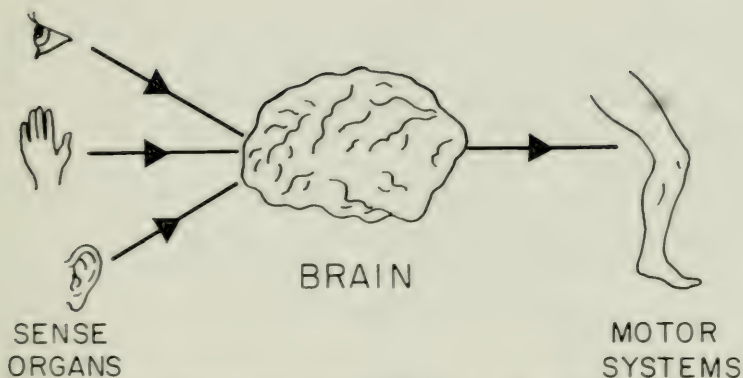


Fig. 2. Diagrammatic representation of an entity lacking insight.

eyes, with the aid of a mirror, to observe his own eyes. Then why should anyone say a person cannot, at least in principle, use his own brain to observe his own brain? All that is required is that nature should have given him the equivalent of an *inner mirror* and an *inner eye*. And that, I think, is precisely what she has done. Nature has, in short, given to human beings the remarkable gift of *self-reflexive insight*. I propose to take this metaphor of “insight” seriously. What is more, I even propose to draw a picture of it.

I would ask you to imagine first the situation of an unconscious animal or a machine, which does not possess this faculty of insight (fig. 2). It has a brain which receives inputs from conventional sense organs and sends outputs to motor systems, and in between runs a highly sophisticated computer and decisionmaker. The animal may be highly intelligent and complexly motivated; it is by no means a purely reflex mechanism. But nonetheless it has no picture of what this brain-computer is doing or how it works. The animal is in effect an unconscious Cartesian automaton.

But now imagine (fig. 3) that a new form of sense organ evolves, an “inner eye,” whose field of view is not the outside world but the brain itself, as reflected via this loop. Like other sense organs the inner eye provides a picture of its information field—the brain—which is partial and selective. But equally, like other sense organs, it has been designed by natural selection so that this picture is a

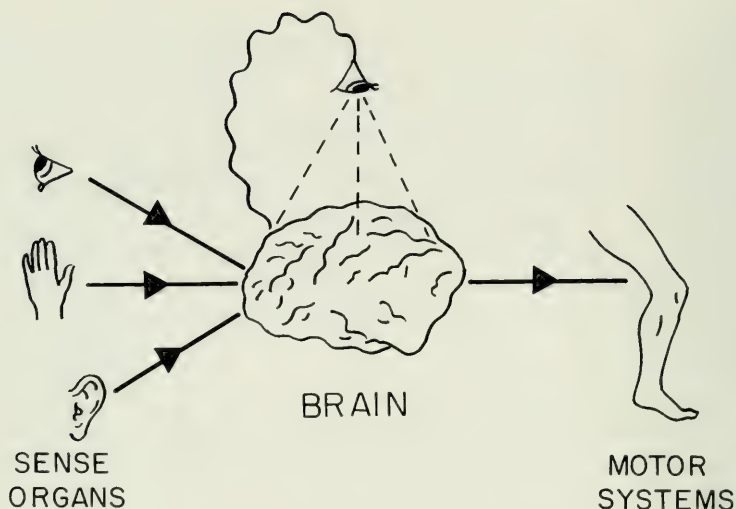


Fig. 3. Diagrammatic representation of an entity possessing insight.

useful one—in current jargon, a “user-friendly” description, designed to tell the subject as much as he requires to know in a form that he is predisposed to understand. Thus it allows him, from a position of extraordinary privilege, to see his own brain states *as* conscious states of mind. Now every intelligent action is accompanied by the *awareness* of the thought processes involved, every perception by an accompanying sensation, every emotion by a conscious feeling.

Suppose this is what consciousness amounts to. I have talked of consciousness as a surface feature of the brain and so I think it is, but you will see now that I’m suggesting it is a very special sort of surface feature, which has in a sense been “super-added.” For consciousness actually is a feature not of the whole brain but of this added self-reflective loop. Why this particular arrangement should have what we might call the “transcendent,” “other-worldly” qualities of consciousness, I do not know. But I would just note that I have allowed here for one curious feature: *the output of the inner eye is part of its own input*. As I expect you know, a self-referential system of this sort may well have strange and paradoxical properties—not least that so-called “truth functions” go awry.¹⁵

Let me recap. We've seen that the brain can do much of its work without consciousness being present; it is fair to assume, therefore, that consciousness is a second-order property of brains. We've seen that Darwin's theory suggests that consciousness evolved by natural selection; it is fair to assume, therefore, that consciousness helps its possessor to survive and reproduce. We've seen that common sense coupled to a bit of self-analysis suggests that consciousness is a source of information, and that this information is very likely about brain states. So, if I may now make the point that immediately follows, it is fair to assume that access to this kind of second-order information about one's own brain states helps a person to survive and reproduce.

That looks like progress; and I think we can relax somewhat. In fact, the heavier part of what I have to say is over. I imagine, though, that you are still feeling thoroughly dissatisfied; and if you are not, you must have missed the point of this whole lecture. I set out to ask what difference consciousness makes, and have concluded that through providing insight into the workings of the brain it enhances the chances of biological survival. Fair enough. But the question, of course, is *how*.

The problem is this. We have an idea of what consciousness is doing, namely giving the subject a picture of his own brain activity, but we have no idea yet about what *biological good* that does him in the wider context of his daily life. It's rather as though we'd discovered that fur keeps a rabbit warm, but had no idea of why a rabbit should *want* to keep warm. Or, to make a more relevant analogy, it's as though we had discovered that bats have an elaborate system for gathering information about echoes, but had no idea of why they should want such information.

The bat case seems to me to provide a useful lesson. When Donald Griffin did his pioneering work on echolocation in bats,¹⁶ he did not, of course, first discover the echo-locating apparatus and then look for a function for it. He began with the natural history of bats. He noted that bats live largely in the dark, and that their whole lifestyle depends on their apparently mysterious capacity to see without the use of eyes. Hence when Griffin began his investigation of bats' ears and face and brain he knew exactly what he was looking for: a mechanism within the bat which would allow it to "listen in

the dark”—and when he discovered such a mechanism there was, of course, no problem in deciding what its function was.

I think this is precisely the tactic we should adopt with consciousness in human beings. Having got this far, we should turn to natural history and ask: is there anything about the specifically human lifestyle which suggests that people, quite as much as bats, possess a mysterious capacity for understanding their natural environment, for which consciousness could be providing the mechanism?

I shall cut short a long story (the substance of two books I have written round this issue¹⁷). When the question is, what would a natural historian notice as being special about the human lifestyle, I'd say the answer must be this. Human beings are extraordinarily *sociable* creatures. The environment to which they are adapted is before all else the environment of the family, the working group, the clan. Human interpersonal relationships have a depth, a complexity, and a biological importance that far exceed those of any other animal. Indeed, without the ability to *understand, predict, and manipulate the behavior* of other members of his own species, a person could hardly survive from day to day.

Now, that being so, it means that every individual has to be, in effect, a “psychologist” just to stay alive, let alone to negotiate the maze of social interactions on which his success at mating and breeding will ultimately rest. Not a psychologist in the ordinary sense, but what I have called a “natural psychologist.” Just as a blind bat develops quite naturally the ability to find its way around a cave, so every human being must develop a set of natural skills for penetrating the twilight world of interpersonal psychology—the world of loves, hates, jealousies—a world where so little is revealed on the surface and so much has to be surmised.

But that, when you think about it, *is* rather mysterious. For psychological understanding is immensely difficult; and understanding at the level that most people clearly have it would not, I suspect, be possible at all unless each individual had access to some kind of “black-box” model of the human mind—a way of imagining what might be happening inside another person's head. In short, psychological understanding becomes possible because, and only because, people naturally conceive of other people as beings *with minds*. They

attribute to them mental states—moods, thoughts, sensations, and so on—and it's on that basis that they claim to understand them. "She's *sad* because she *thinks* he doesn't love her," "He's *angry* because he *suspects* she's *telling lies*," and so on across the range of human interaction.

I shall not, of course, pretend that this is news. If it were, it clearly would not be correct. But what we ought to ask is where this ordinary, everyday, taken-for-granted psychological model of other human beings originates. Why do people latch on so quickly and apparently so effortlessly to seeing other people in this way? They do so, I suggest, because that is first of all *the way each individual sees himself*. And why is that first of all the way he sees himself? Because nature has given him an *inner eye*.

So there at last is a worthy function for self-reflexive insight. What consciousness does is to provide human beings with an extraordinarily effective tool for doing natural psychology. Each person can look in his own mind, observe and analyze his own past and present mental states, and on that basis make inspired guesses about the minds of others.

Try it. There is a painting by Ilya Repin that hangs in the Tretyakov Gallery in Moscow, its title *They did not expect him* (fig. 4). In slow motion, this is how I myself interpret the human content of the scene:

A man—still in his coat, dirty boots—enters a drawing room. The maid is apprehensive. She could close the door; but she doesn't. She wants to see how he's received. The grandmother stands, alarmed, as though she's seen a ghost. The younger woman—eyes wide—registers delighted disbelief. The girl—taking her cue from the grown-ups—is suddenly shy. Only the boy shows open pleasure. Who is he? Perhaps the father of the family. They thought he'd been taken away. And now he's walked in, as if from the dead. His mother can't believe it; his wife didn't dare hope; the son was secretly confident that he'd return. Where's he been? The maid's face shows a degree of disapproval; the son's excited pride. The man's eyes, tired and staring, tell of a nightmare from which he himself is only beginning to emerge.

The painting represents, as it happens, a Russian political prisoner, who has been released from the Tsar's jails and come back home. Neither you nor I may catch the final nuance—more information needed. But try interpreting a scene like this *without* reference to



Fig. 4. Ilya Repin: "They did not expect him," 1884. Moscow, Tretyakov Gallery.

consciousness, to what *we know* of human feelings—and the depth, its human depth, completely disappears.

I give this example to illustrate just how clever we all are. Consider those psychological concepts we've just "called to mind"—apprehension, disbelief, disapproval, weariness, and so on. They are concepts of such subtlety that I doubt that any of us could explain in words just what they mean. Yet in dissecting this scene—or any other human situation—we wield them with remarkable authority. We do so because we have first experienced their meaning in ourselves.

It works. But I won't hide that there is a problem still of *why* it works. Perhaps we do, as I just said, wield these mental concepts "with remarkable authority." Yet who or what gives us this authority

to put *ourselves* in *other people's* shoes? By what philosophical license—if there is one—do we trespass so nonchalantly upon the territory of “other minds”?

I am reminded of a story. There was a dock strike in London, and enormous lorries were going in and out across the picket lines with impressive notices: “By the Authority of H. M. Government,” “By the Permission of the Trades Union Congress,” “By the Authority of the Ministry of War.” Among them appeared a tiny donkey cart, driven by a little old man in a bashed-in bowler hat, and on the cart was the banner: “By my own bloody authority.”

That is a good plain answer to the problem. And yet I will not pretend that it will do. Tell a philosopher that ordinary people bridge this gap from self to other “by their own bloody authority,” and it will only confirm his worst suspicions that the whole business of natural psychology is flawed. Back will come Wittgenstein’s objection that in the matter of mental states, one’s own authority is no authority at all:

Suppose that everyone has a box with something in it; we call this thing a “beetle.” No one can look into anyone else’s box, and everyone says he knows what a beetle is only by looking at *his* beetle . . . it would be quite possible for everyone to have something different in his box . . . the box might even be empty.¹⁸

The problem, of course, is not entirely trivial. Strictly speaking, it is true we can never be sure that any of our guesses about the inner life of other people are correct. In a worst-case scenario, it’s even possible that nature might have played a dreadful trick on us and built every human being according to a different plan. Not just that the phenomenology of inner experience might differ from one person to another, the whole functional meaning of the experience might conceivably be different. Suppose, for example, that when *I* feel pain I do my best to stop it, but that when *you* feel pain you want more of it. In that case my own mental model—as a guide to your behavior—would be useless.

This worst-case scenario is, however, one which as biologists we can totally discount. For the fact is—it’s a biological fact, and philosophers ought sometimes to pay more attention than they do to biology—that human beings are all members of the same biological species, all descended within recent history from common stock, all

still sharing more than 99.9 percent of the genes in common, and all with brains which—at birth at least—could be interchanged without anyone being much the wiser. It is no more likely that two people will differ radically in the way their brains work than that they'll differ radically in the way their kidneys work. Indeed in one way it is—if I'm right—even less likely. For while it is of no interest to a person to have the same kind of kidney as another person, it *is* of interest to him to have the same kind of mind: otherwise, as a natural psychologist he'd be in trouble. Kidney transplants occur very rarely in nature, but something very much like mind-transplants occur all the time—you and I have just undergone one with those people in the painting. If the possibility of, shall we call it, “radical mental polymorphism” had ever actually arisen in the course of human evolution, I think we can be sure that it would quickly have been quashed.

So that's the first and simplest reason why this method of doing psychology can work: the fact of the *structural similarity* of human brains. But it is not the only reason, nor in my view the most interesting one. Suppose that all human beings actually had identical brains, so that literally everything a particular individual could know about his own brain would be true of other people's: it could still be that his picture of his own brain would be no help in reading other people's behavior. Why? Because it might just be the wrong kind of picture: it might be psychologically irrelevant. Suppose that when an individual looks in on his brain he were to discover that the mechanism for speech lies in his left hemisphere, or that his memories are stored as changes in RNA molecules, or that when he sees a red light there's a nerve cell that fires at 100 cps. All of those things would very likely be true of other people too, but how much use would *this* kind of inner picture be as a basis for human understanding?

I want to go back for a moment to my diagram of the inner eye (fig. 3). When I described what I thought the inner eye does I said that it “provides a picture of its information field that has been designed by natural selection to be a useful one—a user-friendly description, designed to tell the subject as much as he requires to know.” But at that stage I was vague about what exactly was implied

by those crucial words: “useful,” “user-friendly,” “requires to know.” I had to be vague, because the nature of the “user” was still undefined and his specific requirements still unknown. In the last half hour, however, we have, I hope, moved on. Indeed I’d suggest we now know exactly the nature of the user. The user of the inner eye is a natural psychologist. His requirement is that he should build up a model of the behavior of other human beings.

That is where the natural selection of the inner eye has almost certainly been crucial. For we can assume that throughout a long history of evolution all sorts of different ways of describing the brain’s activity have in fact been experimented with—including quite possibly a straightforward physiological description in terms of nerve cells, RNA, etc. What has happened, however, is that only those descriptions most suited to doing psychology have been preserved. Thus the particular picture of our inner selves that human beings do in fact now have—the picture we know as “us,” and cannot imagine being of any different kind—is neither a *necessary* description nor is it *any old* description of the brain: it is the one that has proved most suited to our needs as social beings.

That is why it works. Not only can we count on other people’s brains being very much like ours, we can count on the picture we each have of what it’s like to have a brain being tailor-made to explain the way that other people actually behave. *Consciousness is a socio-biological product*—in the best sense of socio and biological.

So, at last, what difference does it make? It makes, I suspect, nothing less than the difference between being a man and a monkey: the difference between we human beings *who know what it is like to be ourselves* and other creatures who essentially have no idea. “One day,” Diderot wrote, “it will be shown that consciousness is a characteristic of all beings.”¹⁹ I am sorry to say I think that he was wrong. I recognize, of course, that human beings are not the only social animals on earth; and I recognize that there are many other animals that require at least a primitive ability to do psychology. But how many animals require anything like the level of psychological understanding that we humans have? How many can be said to require, as a biological necessity, a picture of what is happening inside their brains? And if they do not require it, why ever should they have it?

What would a frog, or even a cow, lose if it were unable to look in on itself and observe its own mind at work?

I have, I should say, discussed this matter with my dog, and perhaps I can relay to you a version of how our conversation might have gone.

Dog: "Nick, you and your friends seem to be awfully interested in this thing you call *consciousness*. You're always talking about it instead of going for walks."

Nick: "Yes, well it is interesting, don't you think so?"

Dog: "You ask me that! You're not even sure I've got it."

Nick: "That's why it's interesting."

Dog: "Rabbits! Seriously, though, *do* you think I've got it? What could I do to convince you?"

Nick: "Try me."

Dog: "Suppose I stood on my back-legs like a person? Would that convince you?"

Nick: "No."

Dog: "Suppose I did something cleverer. Suppose I beat you at chess."

Nick: "You might be a chess-playing computer. I'm very fond of you, but how do I know you're not just a furry soft automaton?"

Dog: "Don't get personal."

Nick: "I'm not getting personal. Just the opposite, in fact."

Dog: (gloomily) "I don't know why I started this conversation. You're just trying to hurt my feelings."

Nick: (startled) "What's that you said?"

Dog: "Nothing. I'm just a soft automaton . . . It's all right for you. You don't have to go around *wishing* you were conscious. You don't have to feel *jealous* of other people all the time, in case

they've got something that you haven't . . . And don't pretend you don't know what it feels like."

Nick: "Yes, *I* know what it feels like. The question is do *you*?"

And that, I think, *remains* the question. I need hardly say that dogs, as a matter of fact, do not think (or talk) like this. Do any animals? Yes, there is some evidence that the great apes do: chimpanzees are capable of self-reference to their internal states, and can use what they know to interpret what others may be thinking.²⁰ Dogs, I suspect, are on the edge of it—although the evidence is not too good. But for the vast majority of other less socially sophisticated animals, not only is there no evidence that they have this kind of conscious insight, there is every reason to think that it would be a waste of time.

For human beings, however, far from being a waste of time, it was the crucial adaptation—the sine qua non of our advancement to the human state. Imagine the biological benefits to the first of our ancestors who developed the capacity to read the minds of others by reading their own—to picture, as if from the inside, what other members of their social group were thinking about and planning to do next. The way was open to a new deal in social relationships, to sympathy, compassion, trust, deviousness, double-crossing, belief, and disbelief in others' motives . . . the very things that make us human.

The way was open to something else that makes us human (and which my dog was quite right to pick up on): an abiding interest in the problem of what consciousness *is* and *why* we have it—sufficient, it seems, to drive biologically normal human beings to sit in a dim hall and listen to a lecture when they could otherwise have been walking in the park.

NOTES

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19. *Elements of Physiology*, p. 138.
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BRAIN SIZE AND THE
EVOLUTION OF MIND

HARRY J. JERISON

AMERICAN MUSEUM OF NATURAL HISTORY
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- Paul H. Harvey, *Comparing Brains*; March 20, 1990

*Published versions of these lectures can be obtained from Publications, Dept. of Anthropology, The American Museum of Natural History, Central Park West at 79th St., New York, N.Y. 10024.

**Out of print.

†Published version: *The Brain in Hominid Evolution*, New York: Columbia University Press, 1971.

JAMES ARTHUR

1842–1930

Born in Ireland and brought up in Glasgow, Scotland, James Arthur came to New York in 1871. Trained in mechanics and gear-cutting, he pursued a career in the manufacture and repair of machinery, during the course of which he founded a number of successful businesses and received patents on a variety of mechanical devices. His mechanical interests evolved early into a lifelong passion for horology, the science of measuring time, and he both made some remarkable clocks and assembled an important collection of old and rare timepieces.

Early in this century James Arthur became associated with the American Museum of Natural History, and began to expand his interest in time to evolutionary time, and his interest in mechanisms to that most precise and delicate mechanism of them all, the human brain. The ultimate expression of his fascination with evolution and the brain was James Arthur's bequest to the American Museum permitting the establishment of the James Arthur Lectures on the Evolution of the Human Brain. The first James Arthur Lecture was delivered on March 15, 1932, two years after Mr. Arthur's death, and the series has since continued annually, without interruption.



James Arthur

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INTRODUCTION

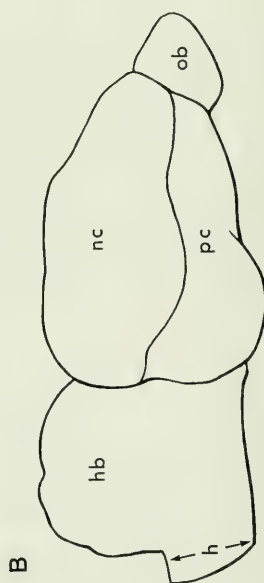
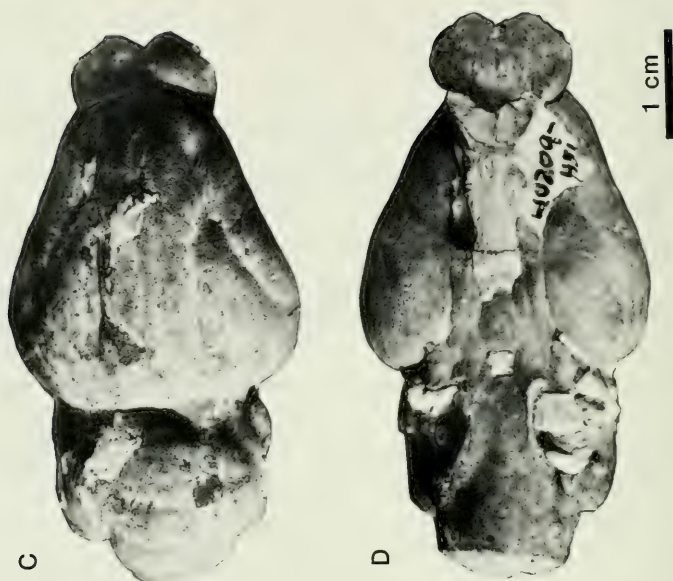
Brain size is important in biology and psychology for many reasons (Jerison, 1987). Tonight I discuss what it can tell us about the nature and evolution of mind. I introduce my analysis by showing data on fossil “brains,” and answering a few simple questions about the data. I want you to have a feel for my material, which is very solid and concrete.

We know a good deal about brain size in living and fossil animals. We also know how to analyze that information to provide a useful picture of a few features of the brain’s work. I will argue that some of the features that can be determined from brain size result in the creation of mind, and that the fossil record of the brain is, therefore, the most direct evidence on the evolution of mind. Let me show you an example of the fossil evidence and the way I use it.

The “brain” in figure 1 is from a fossil ungulate, *Bathygenys reevesi*, an even-toed hooved mammal from an extinct family of the order Artiodactyla. *Bathygenys* lived about 35 million years ago (mya) in the Big Bend area of Texas (Wilson, 1971), and looked something like a miniature sheep—about the size of a domestic cat.

In its external morphology, the brain of *Bathygenys* was similar to brains of living artiodactyls. Neocortical sulci and convolutions visible in the dorsal view (fig. 1C) and structures visible in the ventral view (fig. 1D) could easily be named by using the brain of the tiny living musk-deer, *Moschus moschiferus* (Brauer and Schober, 1970), as a model. In the lateral view (figs. 1A and 1B), we see a “rhinal fissure” separating neocortex from paleocortex. Olfactory bulbs, hindbrain, and the medulla region are also unmistakably identifiable in the fossil as being comparable to those in living species.

The similarities between *Bathygenys* and living species are obviously homologies and are evidence in favor of a uniformitarian (Simpson, 1970) interpretation of the brain of this 35 million year old fossil. Accordingly, we accept the assumption that *Bathygenys*’s brain was organized functionally as well as structurally in ways com-



parable to the brains of its living relatives. We reach the same kind of conclusion from the brains of most fossil mammals when we compare these with the brains of their living relatives.

My analysis of the brain is mainly on changes in its size during the course of evolution and the significance of those changes for the evolution of mind. The analysis begins with the volume of the brain, about 10 cubic centimeters in *Bathygenys*; since the specific gravity of brains is about 1.0, the brain of *Bathygenys* must have weighed about 10 grams, or a third of an ounce. That seems awfully small, but how much should it be expected to weigh? It makes little sense to talk about big brains or small brains unless we have some scale that tells us what is big and what is small.

I mentioned that *Bathygenys* was about the size of a cat, and that is a clue for the second step, which is to establish scales of “big” and “small.” From other data (Jerison, 1973) we know that cats are average mammals in relative brain size, as are most living ungulates. We can, therefore, determine whether *Bathygenys*’s brain was larger or smaller than average (for living species) by comparing it with a cat’s brain. A typical cat’s brain weighs about an ounce; thus, *Bathygenys* had a brain that was about $\frac{1}{3}$ the size of that of an average living mammal of its body size. If we could find comparable evidence in other species, we might conclude that there was an evolutionary advance from a *Bathygenys* grade of relative brain size in the Oligocene to that of average living mammals at the present time.

My raw data and preliminary analysis are as simple as that. I compare many fossils of different geological age with one another, and I anchor my analysis in the data on living species. It inevitably becomes a bit more complicated, because we must determine an “expected” brain size for any animal, regardless of its body size. In the analysis that I just presented of *Bathygenys*, the living cat served as the source of information on expected brain size when body size

←

Fig. 1. Natural endocast of *Bathygenys reevesi*, a Lower Oligocene oreodon (order Artiodactyla). **A:** Lateral view. **B:** Sketch of lateral view to indicate neocortex (nc), paleocortex (pc), hindbrain (hb), olfactory bulbs (ob), and medulla (h). **C:** Dorsal view. **D:** Ventral view. (Specimen UT 40209-431; courtesy of J. A. Wilson and the Department of Paleontology, University of Texas)

was “controlled.” But how does one know that a cat is an average living mammal with respect to the relation of brain size to body size? I discuss this and related questions later, under the heading of “Allometry and Encephalization,” where I review biometric issues.

I have been talking about brains, but you must have realized that the *Bathygenys* “brains” in figure 1 are really oddly shaped rocks. They are casts, “endocasts,” of the inside of the skull. In *Bathygenys* the casting was done by natural agents when the animal died. Its skull was somehow cleaned soon after death, presumably by bugs and microbes that eat soft tissue, and the cranial cavity was then completely filled by sand and debris that fossilized. The filling was shaped like the brain that it replaced, because a mammal’s brain is packed tightly in the cranial cavity and shapes the inner walls of the cavity to mirror a brain’s external surface. The inorganic packing material in *Bathygenys* became mineralized and fossilized into the endocast in the illustration. (Small bits of fossil bone remain attached to the endocast and are most clearly visible in fig. 1D.) “Artificial” endocasts can be made by filling the cranial cavity of a clean skull with latex molding compounds. Regardless of how they are made, endocasts in mammals are usually very similar in both size and shape to the brain and can be analyzed as if they were undissected brains. Under the uniformitarian hypothesis, we assume that this is true for fossil as well as living species.

These hard data, appropriately developed and analyzed, enable us to outline the history of mind as a topic in evolutionary biology. In view of the difficulty of nailing down the concept of mind (cf. Ryle, 1949; Fodor, 1983; Griffin, 1976; Williams, 1985, and many others), however, I have to present my view of the concept in enough detail to be sure that you know what I am talking about.

ON MIND

I identify mind with knowing reality. Bertrand Russell (1912) discussed some of the main issues, and had Immanuel Kant been less categorical, his views on space, time, and objects might also have covered the ground for us. I will not attempt to develop a theoretical picture; that has become the province of a new discipline,

known broadly as the cognitive sciences (Craik, 1943/1967; Johnson-Laird, 1983; Minsky, 1985; Rummelhart and McClelland, 1986, etc.). Rather, for my purpose it is sufficient to take a biological view of the “function” of mind, that is, of the way “knowledge of a real world” serves as an adaptive device.

The reality that we know is most obviously the external world of immediate (conscious) experience. There is also the reality of an internal world of mental images, memories, dreams, thoughts, plans, feelings, etc. Perhaps the most real of all objects in these worlds is the self—which is an “object” on the boundary between the internal and external world and part of both. There is, finally, the issue of consciousness as a feature of mind, but it will be easier to discuss that later, after discussing the brain’s work.

As a first approximation, most of our knowledge of the real world can be understood to result from adaptations that are usually categorized as sensing and perceiving. I begin the story of mind with these categories, because sensation and perception involve important and often unsuspected cognitive dimensions (Carterette and Friedman, 1974). Let us consider as an example a “simple” sensation: the experience of sensory thresholds. How strong must a sound or light be for it to be just audible or just visible? One of the surprising discoveries of sensory psychology is that to understand these thresholds one needs more than information about the strength of the sensory stimulus. Whether you can report that you hear or see weak signals turns out to be determined not only by the strength of the signal, but also by your knowledge of the “value” of a detection, of the “cost” of a wrong report, and of the frequency with which signals are likely to appear (Swets, 1964). These kinds of knowledge are usually thought of as higher order cognitive activities compared to merely sensing a signal. It is evidently appropriate to think of a *sensory-cognitive* dimension of mind, rather than pure sensations that are to be combined by “mental chemistry” to create mind (see Boring, 1942).

There is a stability about our experience of the external world, a “constancy” (Koffka, 1935), which is a major perceptual elaboration of sensory functions. For example, a coin remains a coin in our immediate experience whether it is seen head-on and is sensed as

circular, or whether it is rotated and sensed as elliptical. Processes of this kind, when simulated on computers, are called “pattern recognition,” and the simulation requires *much* more computer power than simulating the more usual candidates for examples of human intelligence, such as proving theorems in symbolic logic. Contrary to our intuition, perception may be harder than “pure thought,” if computers are reasonable models of the mind (Minsky, 1985).

We are misled, because we believe intuitively that things that are easy to do require little processing machinery. Perception, which is immediate and instinctive according to our intuition, would seem to require less brain tissue than complex thought. A more correct view, however, is that perception seems easy only because brains are built to do it, to handle information about the external world. Complex thought is hard, because, despite its size, the mammalian brain did not evolve as a specialized thinking machine. There are unlikely to be many fundamental neurobiological adaptations that are designed specifically for thinking hard about abstractions.

The amount of tissue that is actually devoted to a process in a living brain should be determined by how much tissue is needed to do it well, and how important it is to do it well. If a process is very important but requires a lot of neural machinery, then it might be worth a heavy investment in the machinery to do the job right. That is the correct way to think of the neural control of perception and of the brain’s role in perceptual activities. The activities are so important to mammals that brains have become significantly enlarged to support them.

I trust that you realize that I have now begun to discuss mind-brain relations and the evolution of mind. I have proposed that brains are specialized to process the sensory and perceptual information that provides knowledge of the external world, and I have invoked the idea of selection pressures (“activities so important to mammals”) and affirmed that there must have been a selective advantage, in a Darwinian sense, to have such knowledge. Furthermore, I have invoked the idea of evolutionary change with the words, “have become.”

But I am getting ahead of myself. To complete this statement on mind, I will review the words I use to define its dimensions and to

serve as my vocabulary for categorizing the brain's work. Since our concern is with the knowledge of reality, the basic word in the vocabulary is cognition, which means knowledge, and the basic idea is that a large fraction of the brain's mass is involved in cognition. Perception is a subset in the cognition category and might include mental images generated by language and memories, as well as those generated by sensory data. Memories and thoughts are also subsets, and I suppose that dreams and hallucinations might be sets within the set of mental images. Although we may distinguish these sets from one another, I am unsure about the extent to which they are biologically distinct, or the extent to which they are controlled by different brain structures.

In emphasizing perception I emphasize *experience* rather than behavior. But it is also possible to describe mind with purely behavioral categories. Among the categories that have been most important in discussions of the evolution of mind, I will discuss, briefly, learning, social behavior, and communication, all of which can be defined objectively, that is, with reference only to externally observable behavior.

These behavioristic categories are not independent of perception or of one another. Learning in natural settings is frequently social learning. Social interactions usually depend on perception and communication. Perceived "objects" in the external world are often other living creatures, which may be communicating with the perceiver. And animal communication is by definition a social interaction. Finally, although early ethological studies emphasized innate aspects of behavior, it is now a commonplace of animal behavior studies that some kind of learning (at least "imprinting") is critical for establishing almost all behavior (see Eisenberg and Kleiman, 1983).

The interdependencies transcend behavior. Mature nervous systems in vertebrates are produced by epigenetic systems based on the interaction between growing neural units and the environment in which they grow. A mammal, for example, cannot have a normal brain unless it develops in its normal environment (Hubel, 1988; Rauschecker and Marler, 1987; Udin and Fawcett, 1988; Wiesel, 1982). In an analysis of mind we must deal with complex interactions between nature and nurture, and it is simply foolish to emphasize

one at the expense of the other. It is equally foolish to assume that we can establish categories of mind that function independently of one another. We nevertheless need the categories to organize our thinking about mind.

Categories in the Analysis of Mind: Learning

Learning is probably the most frequently considered dimension for the evolution of mind. It usually appears in the older evolutionary literature as a statement about adaptability. For example:

The criterion of mind . . . to which I shall adhere throughout the present volume is as follows:—Does the organism learn to make new adjustments, or to modify old ones, in accordance with the results of its own experience? (Romanes, 1883/1895, pp. 20–21)

Learning was defined scientifically at the turn of the century, when it was studied in the physiological and psychological laboratory (Pavlov, 1904/1928; Thorndike, 1898), but it has proved to be a disappointing category for evolutionary analysis. The failure was stated most strongly by Macphail (1982) who reviewed the literature on laboratory studies and concluded that vertebrate species are remarkably similar in learning ability. (He considered these as studies of intelligence, and therefore asserted that nonhuman animals were remarkably similar in intelligence—a misleading statement, in my view, because of his narrow definition of intelligence. See Jerison, 1984.) In a series of rigorous experiments on comparative learning ability, Bitterman (1988) found (to his and everyone else's surprise) that essentially all of the "higher order" learning abilities known from laboratory work with mammals were also demonstrable in honey bees. Although his results are interpretable as extending Macphail's conclusion about learning to nonvertebrates, Bitterman prefers the view that they represent convergent evolution.

One problem with learning as a category is inherent in the strict behaviorism that has been the philosophy of its analysis in the psychological laboratory. The analysis is restricted to input and output—stimulus and response—and laboratory settings are designed to control these in the interest of rigor. So constrained, learning is

only marginally useful for an analysis of mind, because the acceptable phenomena for analysis are limited to a very small number of responses (usually two) that are recorded under a very small set (also usually two) of stimulus conditions. The input-output relations in different species can be assigned to the same "learning mechanisms," even if there are very different kinds of information processing inside the intervening black box that is the brain. Dramatic graphs have been published to show that, e.g., a "variable interval" reinforcement schedule produces behavior that is described by a characteristic performance curve, whether generated by a rat pressing a lever for food reinforcement or by a human pressing a lever for reinforcement by the appearance of a target signal (Skinner, 1957). However, it would be naive to conclude that all of the mental (or neural) processes associated with the behavior that underlies the performance curve are identical in rats and humans or that the curves give more than restricted evidence on the nature of mind.

Our present understanding of the nature of learning raises a more fundamental problem for using learning to understand the evolution of mind. The phenomena of learning are explained in terms of a limited set of paradigms: habituation, sensitization, and classical and instrumental conditioning. (Macphail discusses higher order phenomena, but these can be "reduced" to the simpler paradigms.) Although the procedures in these paradigms raise complex issues in the analysis of the behavior (Mackintosh, 1974; Rescorla, 1988), the basic mechanisms seem to be limited to changes in excitability at the synapse (Hebb, 1949; cf. Rauschecker, 1989) and should be identifiable in all organisms with synaptic nervous systems. In evolutionary perspective one must assume that the genetic programs for these fundamental mechanisms appeared early in metazoan evolution and have been retained in all later metazoan species. As basic characters in metazoans, learning mechanisms cannot be used in the analysis of the diversification of species in mental characteristics, except to identify these mechanisms as a common feature in all metazoans in which we assume that the character, "mind," is present. (Cladists might describe these fundamental mechanisms of learning as plesiomorphies, which provide no information for a phylogenetic analysis; see Cracraft and Eldredge, 1979.)

Categories in the Analysis of Mind: Social Behavior

Social behavior as a source of evidence of mind can be subjected to a critique much like that just presented for learning. All multicellular animals are social to some extent. And although the analysis of their social behavior is a rich source of information on the varieties of adaptations (Allee, 1931; Wilson, 1975), social interactions are generated by many different mechanisms, most of which have little to do with mind. These mechanisms are different in different species and are useful for the analysis of phylogenetic relationships, but they may provide little or no information on how mind evolved.

I will illustrate this point with one "nonmind" mechanism among those that are treated in the study of instinct in the classic ethological literature (Lorenz 1935/1937; Tinbergen, 1951). Hailman (1967) analyzed pecking by gull chicks at the adult gull's bill, a "fixed action pattern" that is a necessary part of the social interaction between parent and offspring during feeding. He was able to demonstrate that some stimuli, quite unbeaklike to the human eye, were more efficient ("superstimuli") at releasing the pecking behavior in chicks than was the beak itself. The parent gull's beak is evidently not the "object" at which a chick pecks. Rather, the pecking is released by a configuration of stimulation that is approximated well by the parent's beak, but there are better approximations that can be made by other configurations. The chick is not "pecking at a beak." It is "pecking in response to a configuration." The beak is not an "object" in the chick's world. In this setting, the chick is an automaton, responding in a reflex way to a stimulus complex.

(Phenomena such as these force us to keep a distinction between sensation and perception in some form for the analysis of mind, because the sensory response to an external stimulus is not necessarily organized into a "percept" characterized by constancy effects.)

It is not clear how much of animal social behavior is controlled by nonobject signs in the environment, but ethological analysis suggests that such "sign-stimuli" that cannot be described as objects are typical governors of social behavior in nonhuman animals (Smith, 1977). Their role is usually underestimated in human social interactions, even though our social behavior also often depends signif-

icantly on communication with nonmind "body language," the sign-stimuli of human behavior.

Social behavior involves mind when it involves *knowledge*. To be relevant for mind, social behavior must be based on perceptions of other animals as objects that keep their identities under many transformations, and of signals as having meanings that are related to one's knowledge of the external world. Cognitive factors in social behavior are usually perceptual factors, which enable animals to know (recognize) other animals and events in their social world.

To clarify the distinction between mindless and mind-relevant events, it may help to mention an interesting example of social behavior in which mind is almost certainly important. African green monkeys (vervets) have a repertoire of three different vocal warning signals, which they perfect (by learning and imprinting) during infancy and childhood, and they use these to warn members of the troop of the presence of their three major predators: eagles, leopards, and snakes. From carefully reviewed anecdotal as well as observational and experimental evidence it seems clear that although the signals are stereotyped, the information in these warning signals is of a picture of the external world rather than stimulus configurations that release fixed action patterns (Cheney and Seyfarth, 1985; Marler, 1983). These signals send messages that may have some of the features of natural human languages as communication systems.

Categories in the Analysis of Mind: Communication

Like the example of vocal communication among vervets, most animal communication is typically with a fixed set of stereotyped signals. The signals are often morphological: rump patches in ungulates that are exposed by "tail flagging" to serve as alarm signals (Smith, 1977), hair crests in carnivores used as "intimidation structures" (Wemmer and Wilson, 1983), odors in territorial marking, trail marking, sexual signals and aggressive signals (see Eisenberg and Kleiman, 1983; Gorman and Trowbridge, 1989; Müller-Schwarze, 1983). Vocal signals are, of course, also morphological in that they are constrained by the design of sound-generating organs, although their correct production and use are frequently dependent

on some kind of learning. But whether learned or innate, in most species vocalizations are stereotyped and automatic signals that control social interactions, such as parent-infant relations, warning, threat, courtship, etc. (Gould, 1983).

It is almost a principle in ethological analysis that simple signals by one animal can release complex behavior in another (Maynard Smith, 1978). The gull's beak as a sign-stimulus is relatively simple to analyze, especially when it is recognized that its effectiveness is due to fairly simple stimulus properties and not to its character as an object in the chick's world. The chain of responses that follows is more complex, consisting of the chick's pecking and eventual feeding. In adult vervets, the alarm call is acoustically stereotyped and in that sense fairly simple. The response it elicits in other monkeys is complex, involving evasive movements of running, climbing, jumping, etc., with the paths determined by the immediate environment and the information (a choice among just three alternatives) provided by the call.

In thinking about the evolution of communication as a category of behavior, we recognize that selection should be for accuracy and simplicity. The signals should be uniform and unequivocal, consistent with the simple messages that are usually transmitted, hence the value of morphological signals. The important requirement is that there should be minimal uncertainty about the significance of signals. Neural control of such a signaling system could be fairly simple, requiring a relatively small investment in neural machinery.

As a category of mind, communication and the neural adaptations associated with it is one that students of human evolution are inclined to emphasize, because of the importance of language as a human adaptation for communication and the uniqueness of language as a human trait. The requirements for reliability in animal communication systems, however, are not met by human language, which is notoriously subject to misunderstanding. Partly for this reason it seems likely that human language had different biological roots from those typical for animal communication. I will argue that brain functions in language can be understood only if the human language system began to evolve in the earliest hominids as a cognitive system in response to selection pressures for improved knowl-

edge of the external world, rather than as a system devised for improved communication with other individuals. I will argue that only later (though not much later) in hominid evolution did language begin to evolve into the tool for communication that it is now. As in some of my other propositions about mind, this argument depends on features of brain organization and functions, which I consider in later sections, as well as the peculiarities of language when compared to typical animal communication.

The Function of Mind

Having rejected behavioristic dimensions of mind, let me treat our topic in the conventional functional terms of evolutionary biology by asking how “mind” functions as an animal adaptation. The alternative to mind is a Cartesian reflex machine. Why have mind—a knower of reality? The answer is relatively easy. With the exception of a few sessile species, most animals move about and need information about the external world to guide their movements. “Mind” is one of the adaptations that evolved to handle such information.

In species in which the behavior repertoire is small and the environment predictable, action and reaction, stimulus and response can be tied to one another directly, by reflex mechanisms, to ensure appropriate behavior. Many vertebrate behaviors are of this type: tight bonds between stimulus and response. Frogs and salamanders catching passing insects with flicks of the tongue are classic examples (Ewert, 1974; Lettvin et al., 1959; Roth, 1987). The response is elicited by any small dark object moving at appropriate speed in the animal’s visual field. In nature, most small dark moving objects are things like flies, and the tongue-flicking is an effective “mindless” way to insure a balanced diet.

Mind evolved to handle stimulus-response contingencies where reflex control would fail. This could occur when the information in signal and response was too great to be handled by a purely reflex system. The problem was how to handle very large amounts of biological information. To analyze it we need answers to some specific questions: What are the units of information for the organism? How is information partitioned, categorized, or organized? And

when is there too much information to handle with reflex mechanisms? Although there are elegant analyses, especially of the first two questions (e.g., Miller, 1956; Simon, 1974), an information overload cannot be analyzed without considering the biological limitations of the organ that processes the information, namely, the brain. The complete answer requires a review of the mind-brain problem, but we can indicate a few preliminaries.

Like all large information processing systems, the mind must be organized hierarchically. Information is processed in stages, which correspond to the hierarchical organization of the brain. Biologically, information from the external world is first transformed from physical energy into sense cell activity, and then it is processed and transmitted through a cascade of structures in the nervous system. From the perspective of mind as I have been discussing it, the later stages of processing transform the information from patterns of neural data into a representation of an external world.

The later stages are perceptual and cognitive, and their special feature is that information is organized into chunks (Simon, 1974) or packets, which can represent objects, space, time, etc., that are invariant under many transformations. It is beyond the scope of my discussion to treat the information and its transformations in more detail; there is an impressive literature on exactly that (e.g., Longuet-Higgins and Sutherland, 1980), and possible mechanisms for generating the invariances for visual perception have been described with unusual precision (Marr, 1982).

Although I discuss consciousness in more detail later, I can note that the packets would also organize the contents of *conscious* experience. There is an aura of mystery about consciousness, and I want to conclude my statement on mind by questioning the appropriateness of that aura. How would one suppose that an animal's information processing machinery would be organized to manage the job of living and moving about in the external world? If its possible movements are restricted and the relevant features of its world are few, then an animal might function successfully as a reflex machine that responds to stimuli without organizing them into a representation of an external world. But if the animal's life is more complex, a pictorial rendering of an external world is as natural as

any. Consciousness need be no more than the fact that a picture is constructed. There might be various levels of organization, or complexity, of the representation, but why the mystery? Consciousness can be thought of as an aspect of the organization of information from the external world to cope effectively with the problem of behaving in it. It would be created by the machinery that handles the information, namely the brain, and it would result in easier information processing. The only odd feature is that we must then recognize that the *experienced* real world is a construction by the brain.

THE MIND-BRAIN PROBLEM

If “mind” refers to our knowledge of reality, then the mind-brain problem is: How do brains handle information about the real world, and how does the brain’s processing of neural information correspond to “knowing reality”? Neural information in the brain is measured as weak, usually brief, electrical, magnetic, or chemical signals associated with activity of a nerve cell. Some of the activity originates in stimuli from sensory cells that respond to events in the external environment, but most of the neural activity in the brain results from activation by other neurons. There is a mind-brain problem, because none of the activity of single neurons, not even that generated by sensory cells, is directly related to the real world as we know it. The activity of individual neurons can be recognized as related to events in the real world only if outside observers (usually neuroscientists), who monitor the machines that record the activity of neurons in experiments, can correlate that activity with environmental events. A neuroscientist monitoring the activity of a single nerve cell could not even ascribe that activity to a specific kind of stimulus, such as a sight or a sound, without information about environmental correlates of the activity.

With that limitation in mind, there is nevertheless quite a bit known about how the work of the brain is related to the work of the mind. Although I will obviously oversimplify, let me outline some of the more interesting things that we have known for some

time, about how information in the brain is organized into maps of the external world.

Mapping in the Brain

There are two important ways to think about mapping. First, there is mapping as the work of neuroscientists when recording the results of certain experiments on the brain. The second is to recognize mapping as a feature of the organization of the brain as an information processing system: The brain is to a very significant extent a mapping machine. These are distinct though closely related usages of “mapping,” and recognizing the distinction may help us appreciate some of the features of the mind-brain problem.

The activity of particular neurons in particular regions of the brain can be correlated with particular environmental stimulation, and we can draw a series of maps to record and describe the correlations. The initial map is an undistorted picture of the external environment, and the next maps are projections of the initial map onto various surfaces, beginning with a picture of the external world on a sense organ such as the retina of the eye. Later maps that we draw show the projection proceeding inward to successive regions of the brain and indicate the extent to which the information from the environmental map remains coherent. These maps reflect the information processing going on in the brain and thus suggest the second usage of the idea of mapping.

When we prepare these maps, perhaps the most interesting result is that although the maps drawn on brain areas appear distorted relative to the environmental map, they are distorted in orderly ways. Among the most familiar of the maps are those of the somatosensory system, which are drawn as distortions of a skinned animal or person, with unusual expansion and contraction of some regions. The human picture is a homunculus distorted by having very large thumb, lip, and tongue areas. The same sort of map in other mammals can be prepared more carefully to show more detail. The “animalculus” may seem even odder than the homunculus, because it turns out to be at least twins or triplets, that is, as several copies of the body map (fig. 2).

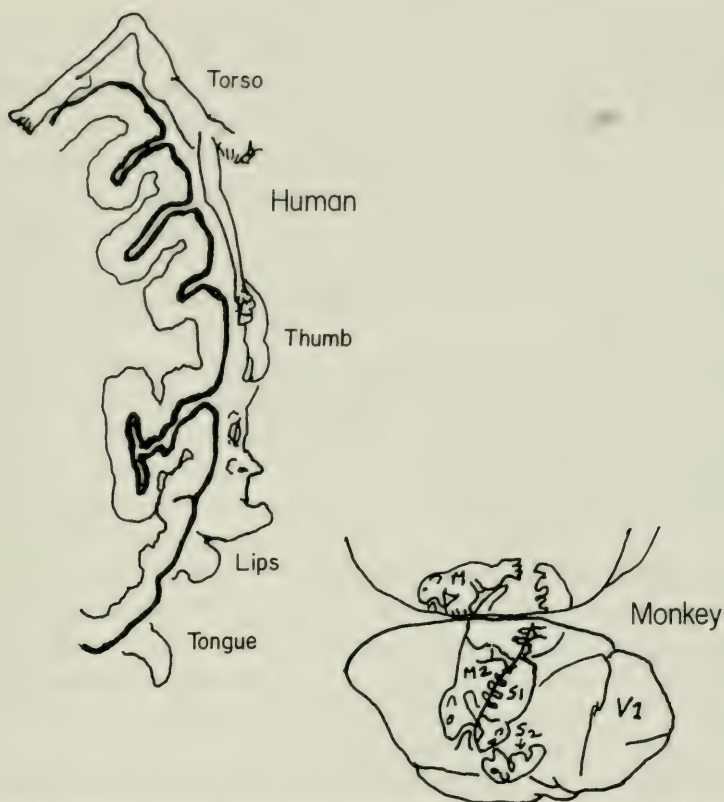


Fig. 2. Maps in the brain. The human map (left) is shown adjacent to a slice of neocortex at approximately *S* in fig. 8, below, where neocortex is about 2 or 3 mm thick. The monkey maps are of two motor and two sensory areas, and are partly on the lateral and partly on the medial surface, shown here on the left hemisphere. (Based on Woolsey, 1958)

The mappings on the brain from the retina of the eye are the most completely studied and best understood (Hubel, 1988), and perhaps for this reason we recognize how unusual a mapping can be. First, these maps, usually called projections, are split between the two halves of the brain, and the details of this split suggest that it is involved in a transformation of data from binocular disparity into a record of the depth of visual space. (The other two dimensions of visual space are encoded by the spatial array of cells in the retina, the locations of which are reasonably well conserved in the spatial

arrangement of neurons at more central neural processing stations.) Splittings occur subcortically and cortically, with major subcortical way stations in the thalamus and the midbrain. There are, furthermore, other splittings of the information from the retina, on color, shape, etc., which are channeled to different layers and regions of the neocortex. There are perhaps a dozen copies of various parts of the map of the retina spread through the visual cortex and the area immediately adjacent to it. In addition, there are major projections of the visual field to other parts of the brain, especially in the temporal lobe.

Other information processing systems in the brain are also very complex. The auditory system has multiple projections through nuclei and tracts in the medulla, midbrain, and thalamus, terminating at several centers in the auditory cortex. Cortical maps project to the cerebellum, and there are recursive systems sending the information back. And all of these maps are connected to one another via assembly points in the hippocampus ("old cortex") and in the prefrontal region of the neocortex (Goldman-Rakic, 1988). I have emphasized sensory and perceptual maps, but motor systems are also mapped systems and support the active manipulation of the environment, which can be crucial for the normal development of the brain as a sensing system (Held, 1965).

This very brief overview of the mapping that is recorded from the brain only begins to suggest its complexity. But in the face of the complexity, it remains correct to generalize about these results as demonstrating a cascade of coherent mappings in the brain of information about the external world.

I began this section by stating that mapping was a way of describing information processing in a brain, but that it was also a fundamental feature of the organization of the brain. This may be obvious from the use of maps to describe what the brain does, but I am concerned that we might miss the significance of our ability to do this. The maps are not mere artifacts that we create in order to understand a complex system. They certainly help at that level, but they can be drawn only because the anatomical system is in fact coherent. There really is a biological wiring system in place, whereby the information transmitted over the "wires" results in a set of mappings that repeat

and analyze sensory and motor maps of the external world. Our artificial “model” of the system—a set of drawings—reflects the neurobiological phenomenon of projection of information from one domain onto another according to fixed rules. These organic maps in the tissues of the brain are aspects of its workings.

In his theory of mind, Kenneth Craik (1943/1967) developed the idea that thinking consists of making models that work in ways comparable to what is being explained (cf. Bower and Morrow, 1990). Similarly, describing the brain’s work as mapping enables us to think about it in terms of a model of how we make a map. We make a map on a piece of paper by drawing lines and points that correspond to features of the external world. Our view of the brain is that it is wired to do this kind of mapping automatically. The brain’s mapping begins with maps of the external world painted onto sensory surfaces, such as the retina of the eye, which are made up of sense cells and closely associated nerve cells. The maps are then projected along nerve fibers, sometimes organized as tracts, which form the “hardwired” system for projecting the maps. Although the fiber pathways may become jumbled, one of the beauties of the system is that it becomes reorganized and again coherent at each of the major “surfaces” at which analysis takes place. In the case of the visual system, for example, fiber tracts often lose their orderly mapped patterns, but order returns at the superior colliculi (mid-brain), the lateral geniculate bodies (thalamus), and in the various maps in the visual cortex.

A map is more than a metaphor for what is going on in the brain. It describes a major feature of the structure of the brain. The cascade of maps in the brain is involved in successive analyses of the data, each analysis extracting or adding features to the information.

A crucial aspect of the brain as a mapping machine is quantitative. How much brain tissue is involved in this work? The mappings occur at sense organs and more centrally at many subcortical and cortical levels in the brain. There is insufficient quantitative analysis of most of the subcortical systems, although mapping almost certainly accounts for a good part of their mass, either as fiber systems transmitting mapped information or as “surfaces” in which the maps can be recorded. There are good data on the neocortex, however,

indicating that most of it is involved in mapping (Jones and Powell, 1970; Diamond, 1979). Since the cortex alone accounts for about 40 percent of the size of the mammalian brain, this means that much of the brain in mammals is devoted to processing information about the external (real) world.

From considerations like these about mapping I have concluded, first, that the elaborate analysis of information about the external world in the brain can be the basis for what we describe as “knowing reality.” The enormous investment in neural machinery in the analysis can be the explanation for some “peculiar” features of our external world, such as its stability in the face of the changing patterns of stimulation at sensory surfaces and the ability to extract precise, deterministic, information from statistical or probabilistic features of neural activity. These stable features of the reality that we know are clearly generated by the work of the brain, and this is part of my meaning in stating that our experienced reality is a construction of the brain.

My second conclusion involves two other features of this activity, which are related to the role of gross brain size as a measure for the analysis of mind. The first of these features concerns the categories of mental activity to which the massive mapping system should be assigned. This is clearly the perceptual-cognitive category, rather than learning, social behavior, or communication. (Perceptual-cognitive dimensions of the latter categories would, of course, be controlled by the mapping system.) The second feature is that the mappings are distributed through much of the brain, and although localization is extremely precise, the maps interact with one another and involve almost all of the mass of the brain. The brain works as a very large “distributed” system involving components present throughout most of the brain (Mountcastle, 1978; Goldman-Rakic, 1988). To sum up, for the mind-brain problem, the analysis suggests that much of the mass of the brain, at least in mammals, is related to perceptual-cognitive adaptations, i.e., for knowing reality.

Consciousness: External Reality

I have used the word “consciousness” several times and discuss some of the issues related to it at the conclusion of the lecture. I

need a few paragraphs here to explain my usage and to show how it fits in with our ideas on mapping and on the brain's work. I distinguish consciousness-as-awareness from self-consciousness, the knowledge that we are knowers. Awareness is the pictorial representation of the real world that we know without special reflection. I believe that awareness in this sense is both more complex and more fundamental a phenomenon than is self-consciousness, which can be analyzed as a type of awareness. My definition of mind as "knowing" reality might suggest that consciousness is necessary for mind. But this is not true. There is excellent scientific evidence of knowledge without awareness, which can be understood only in terms of unconscious processes.

An especially dramatic example is "blindsight" (Weiskrantz, 1986). Patients with partial "cortical blindness" due to lesions in the visual cortex can correctly point to objects that they insist they cannot see—objects that fall in the "blind" region of the visual field affected by their lesion. Their loss of awareness is not accompanied by loss of all information about the location of objects in that region in space. In other words, they "know" features of the external world without being "aware" of them. And the world that they know is mapped like that of the sighted, within the dimensions of time and space rather than by reflex mechanisms.

There is more direct evidence of the mapping of awareness of the external world from the electrical stimulation of the exposed human brain during neurosurgery. Such stimulation can produce a variety of conscious experiences that are determined by the region in the brain that is stimulated and which are often localized in distinct regions of an external world (Ojemann, 1983; Penfield and Roberts, 1959).

Evidence for a "seat of awareness" for *self-consciousness* in the brain is well established and well known in neurology. It is not so much a seat as a nonmapped region, and it also has some paradoxical features, including an odd divisibility. The evidence is clearest in split-brain patients in whom the corpus callosum is cut and who seem to "know" two separate worlds with each half of the brain (Bogen, 1986; Levy, 1988; Sperry et al., 1979), as if there were two minds in one brain. Their worlds refer to different selves, with the

self of the language hemisphere clearly being the self that the patient can talk about, and the self of the other hemisphere identified (by the speaking patient, of course) as a kind of stranger (Dimond, 1979).

A Resolution of the Mind-Brain Problem

The persistent mind-brain problem is, first, how the translation takes place from neurally coded maps into a pictorial world that is experienced as reality. This is the problem of understanding the neural basis of perceptual-cognitive dimensions of mind. I believe that we have an adequate, if not complete, solution of this first problem in the evidence on mapping. But there remains a problem of describing exactly what is mapped, which depends on an analysis of mind that can be related with precision to the brain's work.

We might have the brain generating Kantian categories of mind, for example, and there is no reason to reject this on the basis of current evidence. We do not normally talk of "space," "time," or "object" areas in the brain, but the categories used by neuroscientists could easily be related to Kantian categories. Our direct experience of space corresponds to its projection on the retina on which the visual field is mapped. It is also reflected in the maps projected repeatedly to and from other parts of the brain. The shape and color of objects in the visual field are also mapped at the level of the retina, and part of the depth dimension of visual space is represented as binocular disparity, analyzed at a cortical level. There is no correspondingly direct representation of time in the brain, but a time dimension is involved in the analysis of many signals, especially in the auditory system. There is thus nothing in the structure or function of the brain that eliminates the possibility that part of its work involves the creation of categories comparable to (but not necessarily the same as) those created by Kant. The only problem is with the precise description and understanding of the categories.

Kant's categories are an outstanding achievement of armchair analysis of the nature of mind, but natural categories are almost certainly different. The most important difference is that at least some of the categories that may seem fundamental are species-specific, or "suborder-specific" for us as anthropoid primates. We are

simply too odd a species to be able to use our unaided intuition as a guide to mind in other animals. The metaphor of the mind's eye is a primate's metaphor, which reflects one of the unique features of a primate's world. We say, "I see" to mean that we understand. Were we not primates we might more likely have said, "I smell" (as a transitive verb, of course).

We are odd in at least three ways, two of which we share with other anthropoids (monkeys, apes, and humans) and the third of which is unique. First, while almost all mammals can see, as anthropoids we humans use vision in ways unusual for other mammals. Where ours is a world of colors, most nonanthropoid species live in visual worlds that we would think of as painted in shades of gray. Although color vision is more common in mammals than has been realized (Jacobs, 1981), information from color is not as salient in controlling action in most species as it is in anthropoids. Our second oddity as anthropoids is our insensitivity to the rich world of odors that guides behavior in other land mammals. As anthropoid primates, we might be described as smell blind analogously to the way other mammals are color blind. We receive and use important information when we rely on odors, but our world of odors is not nearly as informative as that of, e.g., cats or dogs or rats, or almost any nonprimate land mammal (Brown and Macdonald, 1985). Our "receivers" for smells, the olfactory bulbs, are a fraction of the size that we would expect them to be at our body size, were we normal mammals (see fig. 12, below).

Our third and uniquely human oddity is that we know the external world through a unique species-typical "sense" that we call language. This is so odd an adaptation that I can discuss its nature and evolution only after presenting more of my analysis of neurobiological and evolutionary issues. It is probably the most important of the species-typical adaptations that affect our armchair choices of "categories."

Our intuitions do not always mislead us about the realities of other animals. There is plenty of evidence that perceptual categories, such as faces or sounds, are known by other species in ways similar to ours. Pigeons are as good as, or better than, people at finding familiar human figures, even well-disguised ones, as individuals in

a crowd (Herrnstein, 1985). It is hard to imagine such a perceptual skill without the availability to the pigeon of a representation of reality that works as well as the human mental image of a person in a crowd. Similarly, although our intuitions are inadequate for us to conjure up a comparable image generated from olfactory information, species that are not smell blind, such as wolves, may know their world with object-specific olfactory images that are as useful as our visual images (Gorman and Trowbridge, 1989; Peters and Mech, 1975; Rasa, 1973; Roeder, 1983).

Regardless of its details, a resolution of the mind/brain problem includes the conclusion that the real world *as known to an animal*, including the human animal, is a construction of its brain and, therefore, that the mind is a construction of the brain. An enormous amount of information has to be processed to generate this construction, and this processing capacity evolved as the brain evolved to larger sizes.

BRAIN SIZE AND PROCESSING CAPACITY

Among the many important facts about brains, I emphasize that much of the brain's enormous capacity to process information is organized in the form of mappings of the external world. In this section I provide quantitative estimates of these features. I show how and why the information processing capacity of a mammalian brain can be estimated from gross brain size, and consider questions of the uniformity of the organization of the brain. The answers enable us to evaluate the utility of brain size as an overall measure of the brain's functional capacity. They provide the basis for steps from a quantitative analysis of the evolution of brain size to statements about the evolution of processing capacity and other brain activity related to "higher mental processes."

Even a mouse's brain is an enormous information processing system. Schüz and Palm (1989) have recently shown that there are about 10 million (10^7) neocortical neurons and an additional 30 million neurons in other brain structures (mainly in the cerebellum) in the mouse. Their truly astonishing figure is on the number of connections among neurons. There are more than 80 billion

(80,000,000,000 = 8×10^{10}) synapses in the neocortex! This in a brain that weighs half a gram: a fiftieth of an ounce. If things were simply proportional when comparing brains, the human brain, which typically weighs about 3 pounds (1.4 kg), would have a total of about 100 billion (10^{11}) neurons and about a quadrillion (10^{15}) neocortical synapses.

Quantitative Implications of Neocortical Organization: Mapping

The brain's business is packaging, organizing, and managing the flow of information that is related directly or indirectly to events in the external world. Much of the information is organized into maps such as those summarized in figure 2, and the quantitative question is: how much of the brain is actually involved in mapping, or, as I would have it, in perception and cognition? According to the work mentioned earlier, essentially all of the neocortex is mapped brain. In figure 3 there is more detailed evidence from the brains of tree shrews and bushbabies.

In presenting the data of figure 3, Diamond (1979) suggested that it may be a general rule in mammalian brains that neocortical extent is accounted for almost entirely by projection systems. He argued, further, that the categories "association" and "projection" are not really appropriate for describing structure-function relations in the brain, and I accept his position. But the categories may be too deeply embedded in our view of both brain and mind to be discarded (they are relics of the "mental chemistry" psychology of the 19th century). It is not difficult to retain the words to describe functional, but not structural, categories. It would be correct to consider association systems as intercalated within and among projection systems; the two would then be mapped as overlays rather than as separated areas. The intimate connections between these systems suggest that neocortical function, in general, should be thought of as related to analyzing information about the real world, although there are, perhaps, different levels of analysis provided by the intertwined "projection" maps and the "association" maps.

I am not proposing a view of how the brain's analysis is organized with respect to projection and association. My concern is with what

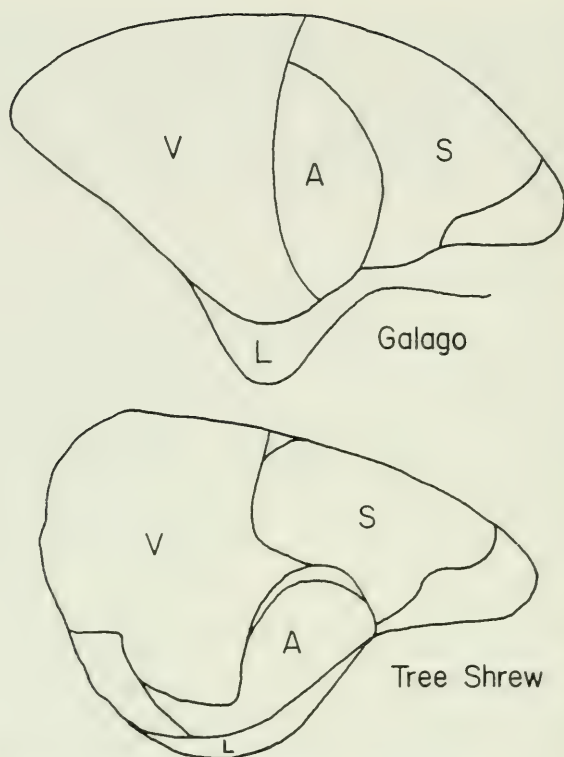


Fig. 3. Sketches of the lateral surface of the neocortex of the right hemisphere in the bushbaby (*Galago senegalensis*) and the left hemisphere's in the tree shrew (*Tupaia glis*), traced from Diamond (1979). V, S, and A refer to projection fields of the visual, somatic (sensory and motor), and auditory systems. Regions without letters had not been assigned to projection systems at the time of Diamond's review. "Old cortex" (L = limbic) is also labeled, though it is not considered in this context. Note that essentially all of the neocortex is mapped brain in these two species.

is being analyzed, which is information from the real world. In addition, I want to emphasize the extraordinary size of neocortex, as a specialized "organ" for perception and cognition, which implies that the amount of processing capacity required to analyze this information is very great.

This conclusion has important implications for our inferences about the enlargement of the brain in mammalian evolution beyond that associated with body size. This increase in *relative* brain size,

which is called encephalization, was driven by the expansion of the neocortex, according to the evidence from fossil endocasts (Jerison, 1990; Radinsky, 1979). The evolution of encephalization may, therefore, be interpreted as having provided neural machinery for more elaborate analysis of information about the external, or real, world. This is the logic behind the idea that mind, i.e., the capacity for "knowing reality," evolved as species became more encephalized. To extend the argument, I point the arrow for causal inference both ways, to suggest that whenever an evolutionary trend toward encephalization can be detected, the most likely explanation for the trend is that there was selection for improved (or at least different) ways of knowing reality.

Quantitative Implications of Neocortical Organization: Packing Units

The neuron and the synapse are often thought of as morphological units of information processing in the brain. A popular third candidate is the module, which in the neocortex consists of a column of tissue in the brain that covers the full depth of neocortex, perhaps 0.5 mm in the mouse or 3 mm in man. A columnar module may be about 0.5 mm in diameter in all species (Hubel, 1988; Mountcastle, 1978; Szentagothai, 1978; this uniformity is only approximate). Columnar organization occurs elsewhere in the brain as well (Scheibel and Scheibel, 1970), but it is in the neocortex that it has been studied most thoroughly and is the model for a modular unit that is involved in the brain's analysis of information (Eccles, 1979). If we take the column as the unit, then the processing capacity of the brain would be proportional to the number of columns, and the number of columns in a brain would be proportional to the surface area. Differences among species in surface area would estimate differences in processing capacity.

If we take the number of neurons as our measure, we are also led to the cortical surface area as a measure of processing capacity. Rockel, Hiorns and Powell (1980) reported that the number of neurons under a given area of neocortex in the brains of very different mammalian species was remarkably constant at somewhat under

150,000/mm². (This implies almost 30,000 neurons in a typical column.) The total neocortical surface area would therefore estimate the total number of neurons in the neocortex and total neocortical processing capacity. The number of synapses is usually estimated as proportional to the number of neurons; hence these too would be proportional to surface area. The key to a morphological estimate of processing capacity is clearly a measure of surface area.

I have no data on neocortical surface alone, but there are published data on the total cortical surface area in many species of mammals. The areas probably include hippocampus, piriform lobes, and other "old cortex" structures in addition to the neocortex. From a broad information processing perspective, the entire cortex is the major part of the great information processing system that is the mammalian brain, and "old cortex" structures are important components of that system. The "archicortical" hippocampus, for example, appears to be a crucial part of the system for handling certain kinds of memory and of mapping the external environment (O'Keefe and Nadel, 1978; Olton, 1985; Squire, 1987). In any case, my data on surface area are on total cortical surface, not just neocortex, but it is not unreasonable to consider that surface as representing the sum of the areas of the maps in the brain.

Could we make an educated guess about the area of the cortex (the sum of the maps) if we knew only the total size of the brain? Could we determine it in fossil brains? A quantitative question deserves a quantitative answer, and it is presented in figure 4. Our guess would be well educated.

Figure 4 presents data on cortical surface area correlated with brain weight in a very diverse sample of mammalian species. There are encephalized species such as the killer whale, elephant, monkeys, a chimpanzee, and sets of humans and cetaceans, but there are also several supposedly primitive species, including egg-laying monotremes (platypus and spiny anteater), marsupials (opossum and wallaby), and primitive placentals (pygmy shrew and armadillo) to name a few examples.

Technical details about this graph and its equation are reviewed later, in a section on uniformities in the organization of the brain. In a few words, the graph tells you that if you know the brain size

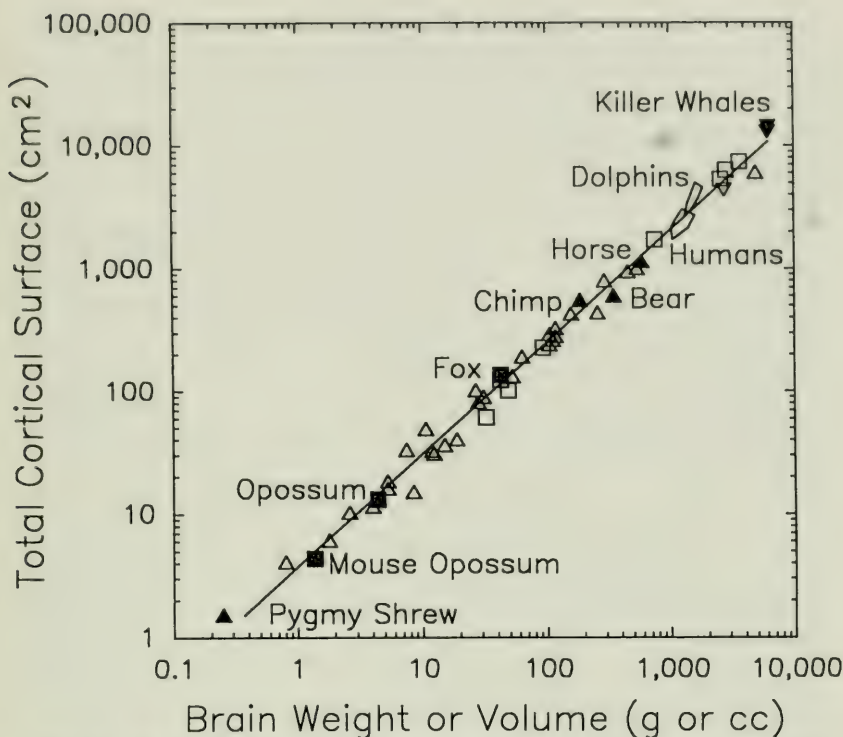


Fig. 4. The relationship between cortical surface and gross brain size “between-species” in mammals. Each point represents a species. In addition, two labeled minimum convex polygons enclose all of the presently available individual data for “humans” ($N = 23$) and “dolphins” (*Tursiops truncatus*, $N = 13$), and probably typify the magnitude of within-species variability. (Δ) Data from Brodmann (1913); (\square) from Elias and Schwartz (1971); (∇) from Ridgway (1981) and from Ridgway and Brownstein (1984). Species named on the graph are also identified by the filled data points. Regression (least-squares fit, assuming errors only in Y): $Y = 3.75 X^{0.91}$, $r = 0.996$, $N = 50$ species.

of an unfamiliar species, you needn’t worry about whether it is primitive or progressive when you estimate the extent of the surface area of its cortex. Your estimate is unlikely to err by more than 1 or 2 percent. Taken together with the relationship between surface area and processing capacity, the message in figure 4 is, therefore, that brain size is a good estimator of total information processing capacity.

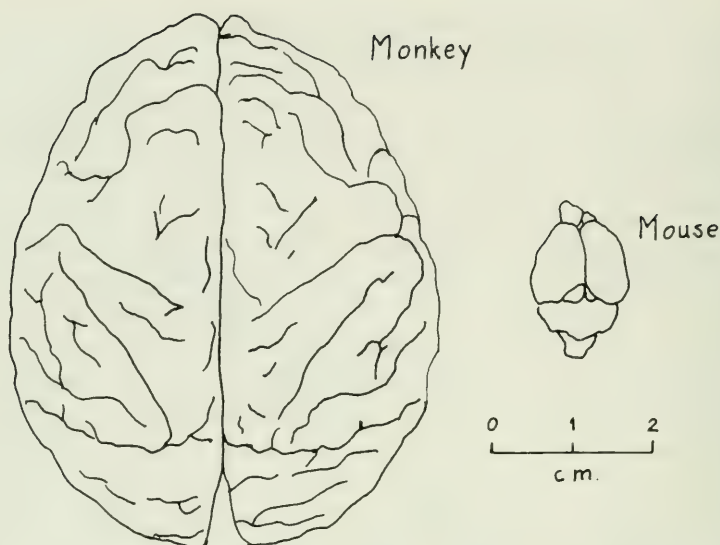


Fig. 5. Tracings from photographs of rhesus monkey and mouse brains (dorsal views) used for electron microscopic data on the corpus callosum. Only neocortex is visible in monkey; parts of the brain in the mouse may be identified by referring to fig. 1B. Both brains are oriented vertically, anterior end up. The mouse structures, anterior to posterior, are olfactory bulbs, cerebral hemispheres (forebrain), colliculi (visible as small exposed structures), cerebellum, and medulla.

Neocortical Organization: Fiber Diameter in the Corpus Callosum

One of the bases for quantifying the information processing capacity of brains according to estimates of the number of neurons that are packed into them is the idea that the cell bodies of neurons are approximately equal in size in different species, and that the number of neurons, independently of their size, can be used to estimate processing capacity. During the summer of 1989 I had a chance to test the hypothesis of uniform cell size in collaborative work with Dr. Almut Schüz of the Max-Planck-Institute of Biological Cybernetics at Tübingen and would like to share the result with you. It is preliminary but convincing. We compared species with impressively different brain sizes: a rhesus monkey and a mouse (fig. 5). The monkey's brain is about 200 times as big as the mouse's: 100 g vs. 0.5 g.

To test the hypothesis most severely, we decided to compare the

diameter of nerve fibers in the corpus callosum in the two species. The corpus callosum is the enormous fiber tract that connects the two hemispheres of the brain, and thicker fibers conduct nerve impulses more rapidly than thinner fibers. Contrary to the uniformity hypothesis, fiber diameters in the corpus callosum might be expected to vary with brain size, because such an adaptation would enable different species to use similar circuitry for at least some sensory and motor coordination. If fiber diameter were correlated with brain size, it would be possible to conserve the same circuitry in species that differ in brain size. To illustrate, if conduction velocity were constant, a message from a neuron in the left motor cortex in a monkey might take 5 msec to reach the right motor cortex, a distance of about 5 cm. A comparable message in the mouse, traversing only, say, 1 cm, would require only 1 msec. If monkeys had larger fibers, they might also be able to transmit the signal in 1 msec. We know that the circuitry is, in fact, similar in different species and that there appear to be no special problems related to conduction velocity. The question is, how were such problems avoided? Was size uniformity sacrificed, or have other mechanisms evolved? Comparing fiber diameter in the corpus callosum of a large brain (as in the monkey) and a small brain (as in the mouse) is, therefore, a good way to examine the hypothesis that uniformity was conserved.

Our preliminary results are in figure 6, which is a montage of electron photomicrographs, two each from mouse and monkey. They suggest that fibers are fairly similar in diameter. If you cover the labels you might still guess which is from monkey and which is from mouse, but I hope that you are impressed by the similarity of the sections. The 200-fold difference in brain size would translate into 35-fold difference in area or a 6-fold difference in diameter, so we would expect the average fiber diameters to be 6 times as great in monkey as in mouse if there were a simple (linear) proportionality with respect to brain size. It is obvious that the differences here, such as they are, are much smaller.

For a quantitative analysis, we measured the cross-sectional areas of the myelinated fibers in both species in sections like those in figure 6. The results were surprising and instructive. They are summarized in figure 7.

Monkey

Mouse

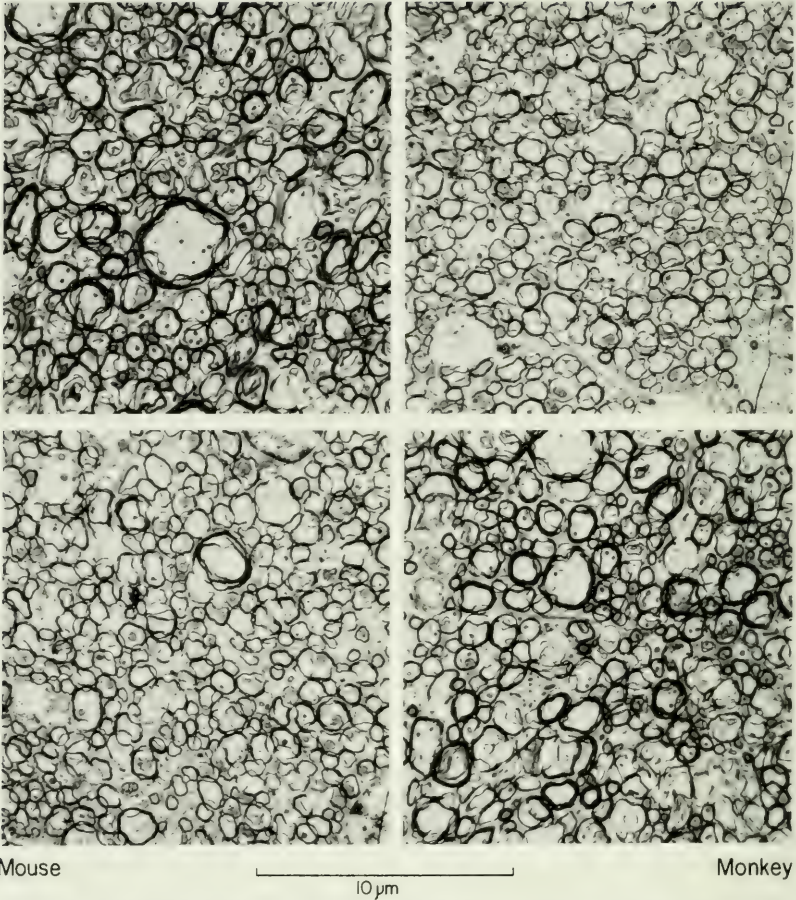


Fig. 6. Electron photomicrographs of cross sections of the corpus callosum in monkey and mouse. (Courtesy Dr. Almut Schüz)

The lower graph is a frequency distribution of the number of fibers that we counted at 0.1 micron-square steps of cross-sectional area in the two species. The modal regions of the distributions for mouse and monkey are surprisingly similar. This is even clearer in the upper graph, in which the relative instead of absolute frequencies of fibers of different cross-sectional areas are compared.

The overall result suggests that only a fraction of the myelinated

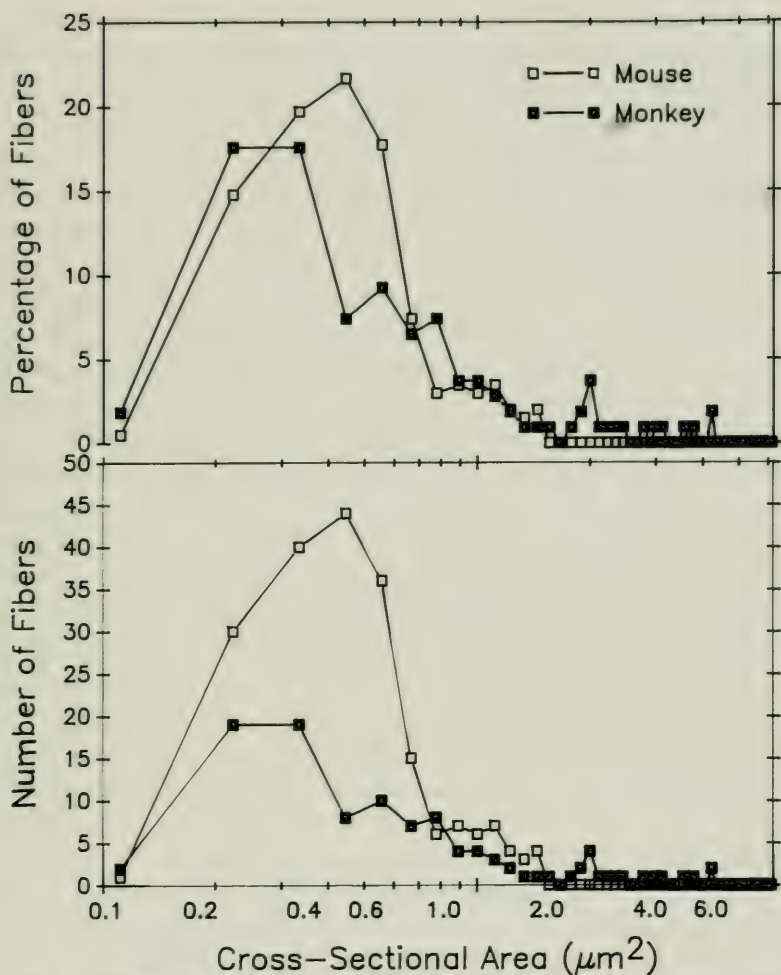


Fig. 7. Relative frequency (upper graph) and absolute frequencies (lower graph) of myelinated fibers of the indicated diameters in the corpus callosum of monkey and mouse. Counts from a total of four sections, comparable to but not the same as those shown in fig. 6.

fibers have to have higher conduction velocities to compensate for the effect of difference in transmission distance between the brains. There may also be important differences in the number of unmyelinated fibers, with many more in mouse than in monkey, and this may be another adaptation for handling the conduction velocity

problem. For my present purpose, however, it is sufficient to examine the data on myelinated fibers. Despite the major “pressure” for increased conduction velocity in monkey corpus callosum relative to that in mouse, the majority of callosal fibers were comparable in cross-sectional area in the two species.

Cell size evidently tends to be constant across species, and since brains are packed efficiently, the amount of neural material per unit volume of the brain should tend to be uniform in different brains. The amount of information that is handled should be proportional to the amount of processing machinery, and larger brains should, therefore, normally have more information processing capacity than smaller brains. The conclusion is the same as that from the surface-volume relationship described in figure 4: Brain size is likely to be a good “statistic” for estimating processing capacity in a species.

The constancy in amount of neural material can be contrasted with the packing density of neurons, which is known to *decrease* proportionally to the cube-root of brain size. In comparisons between mouse, human, elephant, and whale, for example, neuron density is of the order of 100,000 neurons per cubic millimeter of motor neocortex of the mouse, whereas in the three larger brained species it is of the order of 10,000 per cubic millimeter. I have used this relationship to analyze the meaning of brain size (e.g., Jerison, 1973, 1985b) and should reconcile this finding with the idea of uniformity. There is no real contradiction, just a bit of confusion about what a neuron is.

Neuron density is determined by counting neurons that are prepared for microscopy by staining the cell bodies and not the axo-dendritic arborization. In larger brains, the cell bodies are further apart, and this is what the neuron density analysis is about. But if we consider the arborization as well as the cell body of a neuron, the total amount of neural material per unit volume is about the same in all brains, and this is what “packing efficiency” is about. [The average size of neurons is, thus, larger in larger brains, if we include both cell body and arborization; the real constancy appears to be in the number of synapses per unit brain volume. In this connection we should remember that although synapses occur on cell bodies, most of them occur along the arborization (Schüz, 1988).]

When I first analyzed this issue, I recognized that there was an inverse relationship between data on "neuron density" and the "length of the dendrite tree." In a slightly convoluted way, I reached the correct conclusion that the amount of information processed *per unit cortical volume* was constant across species (Jerison, 1973: 70), which means that processing capacity would be proportional to brain size across species.

Remarks on the Corpus Callosum Fibers

While the comparability of data on mouse and monkey was, of course, gratifying support for my basic hypothesis of uniformity, a closer look at the data is also rewarding. I have used the phrase, "as a first approximation," several times, and my general view is that a correct *evolutionary* analysis of mind is probably limited mainly to first approximations. I see mind in terms of "knowing reality," but recognize that the knowledge is likely to take different forms in different species. The "first approximation" would be to the most general features of knowledge, and could refer to between-species aspects of mind, whereas finer analysis would lead to detailed statements that would be needed for an understanding of within-species, or species-typical, adaptations.

For our data on the corpus callosum, the first approximation is in the comparisons involving the major parts of the curves in figure 7, the regions about the mode. Here it is clear that the distributions of fiber cross-sectional areas are remarkably similar, and this argues for a major generating force, or constraint, that works in the same way in very different species, independently of brain size or specialization. The tails of the distributions, however, are clearly different in important ways, which are evident in the data as shown in figure 6, and in the difference between the upper and lower curve in figure 7.

The modal regions of the distributions (areas less than $1300\ \mu\text{m}^2$) are fairly symmetrical about the mode and appear to be approximately log-normal distributions. This is clearly the case for the mouse fibers. A large fraction of the monkey fibers are also represented by the modal distribution, but 15 percent of the monkey fibers were in

the long tail. If one were to prepare a processing model involving the timing of nerve impulses, the correction for faster conduction in the monkey brain would, clearly, involve the activity of that 15 percent. That 15 percent is also the reason for the much smaller absolute frequencies in the modal part of the monkey distribution as compared with the mouse distribution. A total of only 108 monkey fibers were counted on these sections, whereas 203 mouse fibers were counted. The tail of the monkey distribution, that is, the upper 15 percent of the fibers, accounted for more than half of the area of these sections, and that is why there are fewer monkey than mouse fibers in our data set.

A still closer approximation to a complete description of the operating characteristics of the corpus callosum would almost certainly include information transmitted by nonmyelinated fibers, and although these were not considered in this analysis, Dr. Schüz and I are acutely aware of the fact that there were surprisingly few such fibers in the monkey, whereas more than half of all of the fibers in the mouse were in this category. We did not analyze the difference, mainly because we are not certain that it was not an artifact; it is possible that differences between the way that the mouse and monkey material was prepared for microscopy affected the identifiability of nonmyelinated fibers differently from the myelinated fibers in monkeys.

BRAIN ORGANIZATION

The issue that I address now is the extent to which the brain is put together and works the same way in different species. It is important for our discussion, because at some levels of organization, brains of different species are, of course, different, and yet it is the uniformities among brains that enable us to evaluate the evolution of brain size as related to the evolution of mind.

It is not uncommon to hear competent neuroscientists remark that, "Brain size is trivial; it is the organization of the brain that is important." A correct statement is that both size and organization are important in the brain's work, and size is especially important for our understanding of the evolution of mind. Although I will try

not to drown you with data as I present the evidence on the importance of brain size, I am convinced that nothing but data in heavy doses can overcome our prejudices against simplicity (Deacon, 1990), when we try to think straight about the extraordinarily complex system that is the brain. Some things about the brain are in fact fairly simple.

We have seen that brain size estimates the total processing capacity for mammalian brains, and it is this fact that is crucial for our understanding of the evolution of mind. However, processing capacity is allocated to different functions, more or less in proportion to the importance of the functions in the life of a species, a principle that I have called "proper mass" (Jerison, 1973: 15–16). For example, species using auditory information have expanded auditory centers; we as primates are visual specialists and have expanded visual centers, and so on. In spite of such specializations, which occur in some form in all species, the broad outlines of the evolution of mind can best be appreciated from the uniformities, that is, the extent to which brains are organized in the same way, at least as first approximations. The evolution of mind is then seen as a general phenomenon, related to processing capacity, and the evolution of specializations of mind can be understood as specialized adaptations.

My purpose in this section is to describe some of the uniformities of brain organization, while also indicating a few major diversities related to the specializations of different groups of mammals. My evidence on organization is primarily on how the brains of living species of mammals are similar and different in the absolute and relative sizes of their larger parts. I restrict it in this way, in order to be able to apply the evidence on living brains to the data on fossil endocasts. The application is to judgments about the "mind" of an animal such as *Bathysgenys*, which might be based on evidence of its brain as shown in figure 1.

Structural organization can be represented by *allometric* ("quantitative comparison of structures") analyses of the relationships among the parts of the brain. The question in such analyses can be very simple: if one knows the size of one structure, how well can one estimate the size of other structures in a species? For most of the brain, the answer is "quite well." You have seen one example

in figure 4, above, in which 99 percent of the variance in cortical surface area was determined by brain size in 50 very different mammalian species. We could use the results shown in figure 4 to estimate the surface area of the cortex of any mammal. In *Bathysphenys*, for example, the brain weighed about 10 g, and we can, therefore, estimate the area of its cortical surface as approximately 30.7 cm² (see eq. 1, below).

It has been appreciated for many years that at the species level brain size is determined primarily by body size, but that species are also different in *encephalization* beyond the expectations from body size. It is natural to ask whether more encephalized brains are organized very differently from less encephalized brains. The answer seems to be that it usually makes no measurable difference whether a brain achieves its gross size because of allometry or because of encephalization for the gross measures used in most allometric analyses. There are differences among major taxonomic groups, however, some of which will be evident in the detailed analyses that follow.

Uniformities in the Brain: Surface-Volume Relations

One of the most impressive and most important of the structural uniformities in the mammalian brain was displayed in figure 4, above, and it is a good point of departure for a discussion of uniformities and diversity. This graph showed that as a very good first approximation, the area of the cortical surface in mammals is determined by gross brain size. The correlation coefficient of 0.996 means that more than 99.2 percent of the variance in cortical surface is "explained" by brain size. When we look more closely at the data, however, we are rewarded with the surprising discovery that the one percent of "unexplained" variance involves significant deviations from uniformity and is not attributable to "error" in the statistician's sense. The most interesting example is for human data, because it destroys an old myth about our marvelous brains.

The equation shown in figure 4 was calculated as a regression of y on x, which is the proper equation to use to estimate cortical surface in a specimen in which brain weight or volume has been determined. To three significant figures, the equation is:

$$S = 3.749 E^{0.913} \quad (1)$$

Equation 1 enables us to assert that the human brain is less convoluted than one would expect for a mammalian brain of its size. In the analysis that leads to this conclusion, we first determine the relationship between cortical surface and convolutedness, and then we determine our place among the mammals with respect to expectations about convolutedness.

The relationship between surface area and convolutedness is based on the fact that the exponent in Eq. 1 is greater than $2/3$, which implies an orderly change in the shape of the cortex as a function of brain size. If there were no change in shape, the exponent would be $2/3$.¹

The obtained exponent of 0.913 has a standard error of 0.0116; its 99 percent confidence limits are between 0.88 and 0.94—clearly greater than $2/3$. (The probability that the obtained exponent was sampled from a population with a true value of $2/3$ is of the order of 10^{-51} , or about one divided by the square root of a googol—my first encounter with the latter number outside of dictionaries and mathematical entertainments.) The change in the shape of the brain “between-species” as the brain becomes larger is toward more surface in larger brains, a change produced by the appearance of folds, or convolutions, in the surface. The first conclusion from figure 4 is, therefore, that as brains become larger they become more convoluted. The high correlation between surface and volume (log units) indicates that the relationship is very strong and that most of the differences among species in convolutedness are accounted for by the differences in brain size.

A brain would be more convoluted than expected if its surface area were more than that predicted by Eq. 1. We can, therefore, determine whether human brains are unusually convoluted by finding whether they exceed the prediction. My data are on 23 human brains from Brodmann (1913) and Elias and Schwartz (1971). Of these, four had more surface and 19 had less surface than one would

¹For example, the surface-volume measures for all cubes are related by the exact equation, $S = 6 V^{2/3}$, and all spheres—whether the size of a golf ball or of the sun—by the equation $S = 4.84 V^{2/3}$.

expect from eq. 1. The expected division is, of course, 11.5 above and 11.5 below. A chi-squared test of the obtained versus the expected frequency yields chi-square = 9.78, $df = 1$, $p = 0.002$. Thus, there is about 1 chance in 500 that my sample of human brains was from a population that was as convoluted as expected in the sample of mammal brains in figure 4. Not only are our brains not average in convolutedness, they are below par for mammals. But we are close to where we would be expected to be, given the size of our brains, so we needn't go into mourning.

We hardly need a statistical analysis of the dolphin brains described by Ridgway and Bronson (1984). This sample of 13 *Tursiops truncatus* brains is enclosed in the convex polygon labeled "dolphins" on figure 4. All 13 brains had more cortical surface than predicted by Eq. 1. They are clearly more convoluted than expected: chi-square = 13, $df = 1$, $p = 0.0003$. The contrast between the human and dolphin brains in convolutedness is obvious and visible to the naked eye (fig. 8).

These departures from uniformity in brain organization are further clarified by more microscopic analysis. The human brain appears to be a normal primate brain with respect to most features of its organization. The number of neurons under a given area of neocortex is like that of other primates (Rockel et al., 1980), and we shall see shortly that it is a normal primate brain with respect to the sizes of other brain structures relative to the whole brain. Dolphin brains (and, very likely, other cetacean brains) are not like those of land mammals in this respect. The neocortex is thinner, its layers are less clearly defined, and it has only about 2/3 the number of neurons per unit surface area compared to that of land mammals (Garey and Leuba, 1966). Greater convolutedness in delphinids is more than made up for by the less dense packing of their neuronal material.

To conclude, the amount of surface area, and associated convolutedness of the brain in mammals seems to be determined primarily by brain size. (There are other important factors that cause the relationship, which are discussed by Rakic, 1988, and by Welker, 1990; the relationship in figure 4 may be thought of as describing the net effect of the causal factors.) If the neuron is the unit of processing, the processing capacity of a brain is, thus, estimated by

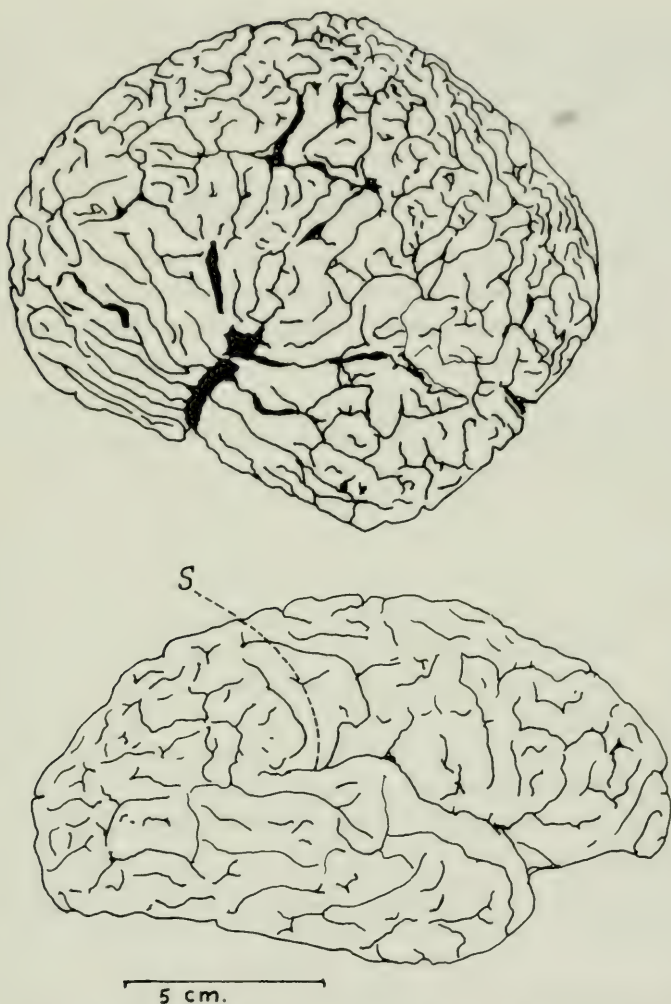


Fig. 8. Tracings of the fissural patterns in lateral aspects of neocortex in man and dolphin. Upper sketch, dolphin (*Tursiops truncatus*) left hemisphere. Lower sketch, human right hemisphere. (From a photograph by Dr. Sam H. Ridgway)

brain size, and this is the outstanding uniformity of organization revealed in this analysis. But even though almost all of the variance in surface area is accounted for by brain size, some of the small residual differences among species are significant. The most surprising of these, perhaps, is that the human brain is less convoluted

than average for mammals. Unless we agree to give up our place at the top of the tree as the wisest of creatures, this should be enough to quash forever the old canard that convolutedness is related to intelligence in animals.

Uniformity and Diversity: Forebrain and Cerebellum

While preparing these notes for publication, I was browsing through a popular but important critique of computational analyses of mind by the physicist, Roger Penrose, and found the following statement about “real brains and model brains” (Penrose, 1989: 375):

The part [of the brain] that human beings feel that they should be proudest of is the cerebrum—for that is not only the largest part of the human brain, but it is also larger, in its proportion of the brain as a whole in *man* than in other animals. (The *cerebellum* is also larger in man than in most other animals.)

I think that this statement is pretty close to conventional wisdom about the human brain, and although it evidently passed the scrutiny of Penrose’s expert consultants in neurobiology, it is misleading where it isn’t wrong. The questions are of the kind that I am reviewing—about clues from the organization of the brain for our understanding of man’s place in nature, and I am pleased to correct Penrose. Is the “cerebrum” the largest part of the human brain? Is it disproportionately large relative to our brain as a whole? And how about the human cerebellum? It is easy to check quantitative relationships like these, and this is the issue that I address in this section.

First, an overview. The cerebrum, which could refer either to the cerebral cortex or to the entire forebrain, is indeed the largest part of the human brain, but it may be important to add that its size follows a single rule for all anthropoids as a proportion of the total brain size. Cerebral cortex accounts for about 40 percent, and forebrain accounts for about 75 percent of the brain’s volume in all anthropoid primates. There is nothing special to be proud of about the human brain in this respect. Our cerebrum is large but not disproportionately large. We are properly proportioned primates.

Like the cerebral cortex, the human cerebellum is also about the size one would expect given the total size of our brain (actually slightly too small relative to other orders, but right for anthropoids).

It accounts for about 10 percent of the brain, and this seems to be the case not only for primates but for all mammals. There is nothing special about the relative size of the human cerebellum. Of course, the human cerebral cortex, cerebellum, and forebrain are among the largest known, but they are very large because the whole human brain is very large, exceeded in size only by the brains of elephants and cetaceans. If we know the size of the whole brain, we can estimate with fair accuracy the size of the cerebellum in any mammalian species.

Now, the data. Stephan and his colleagues (Stephan et al., 1981) have published extensive data on the volume of the brain and many of its parts in 76 species of mammals, and I have reanalyzed and, in some instances, reinterpreted the data from the perspective of organization and reorganization of the brain. The data are on 26 species from the order Insectivora (shrews, moles, and hedgehogs), two Macroscelididae (elephant shrews), three Scandentia (tree shrews), and 45 Primates, of which 18 are from the suborder Prosimii (lemurlike species) and 27 from the suborder Anthropeidea; I have followed Carroll (1988) on nomenclature. I have separated the data on tree shrews in the graphs, but I followed Stephan et al. in treating the elephant shrews as insectivores (omitting them does not affect the results). The tree shrews, which Stephan had included among the primates, are evidently more like prosimians than like insectivores in the absolute and relative sizes of the brain and its parts.

In all of the analyses that I present here, I use either total brain weight or total body weight as the independent variable, since these can be estimated in fossil animals. I am concerned primarily with the pattern of relations of the parts of the brain to those independent variables.

Let us consider, first, the measures mentioned by Penrose. If the cerebrum is interpreted as forebrain it would include all of the cerebral cortex (neocortex, paleocortex, and archicortex, including hippocampus), the basal ganglia, and the diencephalon (thalamus, epithalamus, and hypothalamus). I exclude the olfactory bulbs by analogy with the exclusion of the retina of the eye (also brain tissue, embryologically) as an elaborate sense organ, though many authors would include these as well. The relationship between the volume

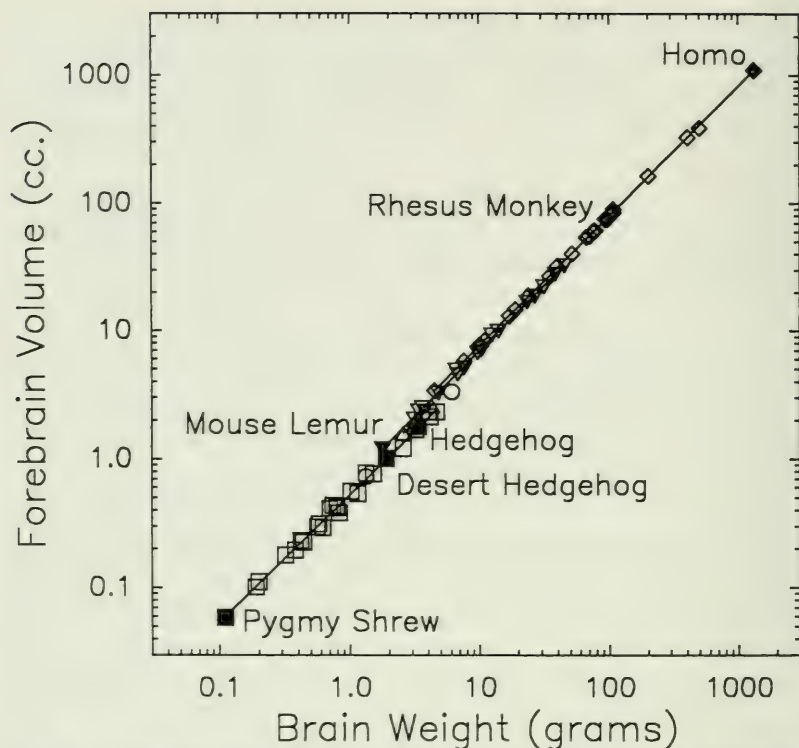


Fig. 9. Forebrain volume as a function of brain size in 76 species of mammals. (\square), Insectivores; (Δ), tree shrews; (\circ), elephant shrews; (∇), prosimians; (\diamond), anthropoids. Regression equations (assuming errors only in Y) and correlation coefficients: entire sample: $Y = 0.56 X^{1.07}$, $r = 0.999$; insectivores: $Y = 0.53 X^{0.99}$, $r = 0.998$; prosimians: $Y = 0.66 X^{1.02}$, $r = 0.999$; anthropoids: $Y = 0.74 X^{1.01}$, $r = 1.000$ ($= 0.9999$). Species named on the graph are also identified by the filled data points. Data from Stephan et al. (1981).

of the forebrain, excluding olfactory bulbs, and that of the whole brain in 76 mammalian species is illustrated in figure 9.

Despite the very high correlation for the entire sample ($r = 0.999$, log data), the slope (exponent) of 1.07 is misleading. It implies that larger-brained species had disproportionately large forebrains because of a single rule about brain size, independent of taxonomic group. In fact, the slopes for each order or suborder were all approximately 1.0, indicating that within each group the forebrain was an approximately constant fraction of the whole brain. The coeffi-

cients tell us what that fraction is. For the higher primates (anthropoids) it is 0.74288 (rounded to 0.74 in the legend of the graph), and this is the basis for my statement earlier that forebrain is about 75 percent of the anthropoid brain.

The point representing human data lies on the line, indicating no positive deviation for us. We are "normal." To illustrate with the actual data, the human forebrain volume reported by Stephan et al. was 1094 cc. The volume estimated from the regression equation for higher primates (exponent = 1.01448; brain weight reported by Stephan et al. = 1330 g) is 1096 cc.

There are statistical lessons for us, comparable to our discovery that even a correlation of 1.00 (0.996 to three significant figures) as shown in figure 4 does not mean that deviations from the regression line, or norm, are not significant. The separate regression equations in figure 9 for insectivores, prosimians, and anthropoids are significantly different from the group regression. Small deviations may signify nonsignificant deviations from a norm, but they may also mean that there are real differences. For these data, the differences reflect the fact that the forebrain is an approximately constant fraction of the whole brain in the three groups for which we have significant amounts of data: 53 percent in insectivores, 66 percent in prosimians, and 74 percent in anthropoid primates, and these are clearly not trivial differences.

I separated the elephant shrews from insectivores in this graph, but you can see that the insectivore regression would account for the elephant shrew data, at least that for the largest specimen. In the remainder of the analysis I treat elephant shrews as insectivores.

The analysis of the size of the cerebellum in these species is presented in figure 10. As in figures 4 and 9, the main message about the cerebellum is the orderliness of its size in this group of mammals, although the pattern of size relationships is reversed. Insectivores seem to be a bit more cerebellarized, as it were, than prosimians, and the anthropoids are the poor relations. The meaning of the relationship is not obvious; cerebellar functions are traditionally thought of as related to motor control, and one might expect the very agile anthropoids to have at least as much cerebellum per unit brain size as the other groups. As one learns more about cerebellar

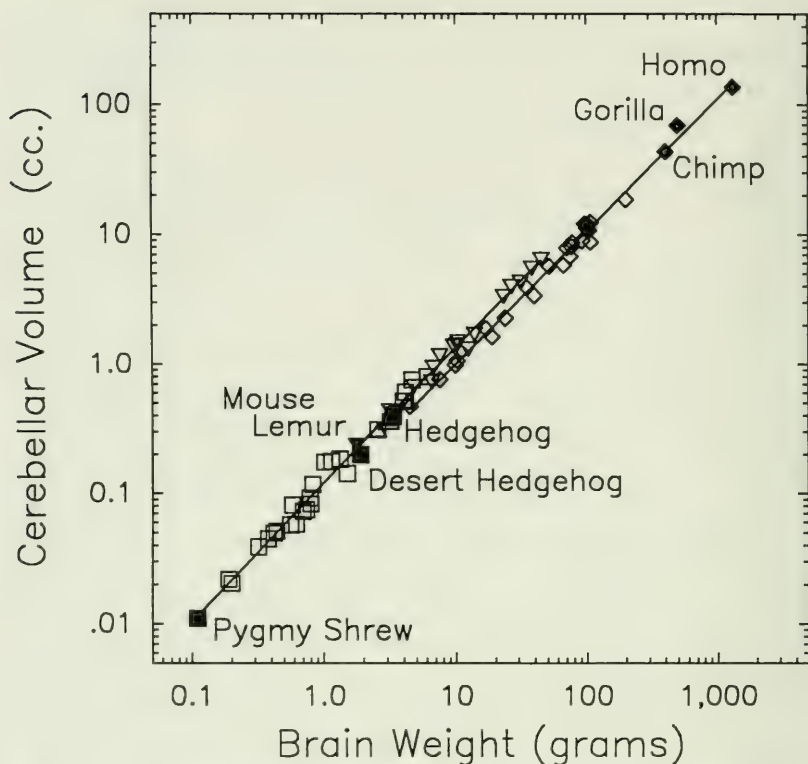


Fig. 10. Cerebellar volume as a function of brain size in 76 species of mammals. Symbols as in fig. 9, except that elephant shrews are treated as insectivores. Regression equations (assuming errors only in Y) and correlation coefficients: entire sample: $Y = 0.12 X^{0.99}$, $r = 0.997$; insectivores: $Y = 0.12 X^{1.06}$, $r = 0.991$; prosimians: $Y = 0.12 X^{1.03}$, $r = 0.995$; anthropoids: $Y = 0.09 X^{1.02}$, $r = 0.996$. Data from Stephan et al. (1981).

functions that are involved in higher mental processes, this is doubly puzzling. But the facts are there in figure 10. We humans are not prize specimens, even among the higher primates, despite our handiness with tools. A little on the numbers: Stephan et al. report the human cerebellum as 137 cc in volume. In anthropoid primates the coefficients for the regression equation are 0.09521 and 1.0201, which would predict the human cerebellum to be 146 cc, so we are a bit less cerebellarized than expected for our group—not significantly low, but certainly not high.

There is a fairly simple explanation for the low “cerebellarization” of higher primates, which has to do more with brain specialization and total brain size than the contribution of the cerebellum to brain size. Anthropoids have unusually large brains for their body sizes—about twice as large as prosimians, for example, and five or six times as large as insectivores. This encephalization in anthropoids is probably related primarily to expanded visual functions and other brain functions in which the cerebellum is only marginally involved. Anthropoid primates are not undercerebellarized. Rather they are overvisualized, as it were, so their gross brain size is greater than one would expect, other things being equal. Using brain size as the independent variable to estimate the size of the cerebellum as a dependent variable is in this case misleading. A better independent variable would be a fraction of the total brain size that would exclude some of the encephalization component in gross brain size that is related to vision in anthropoids.

Although there exist, in principle, better estimators of the size of the cerebellum than total brain size, we should not lose sight of how good gross brain size is as an estimator. We need only keep in mind that the errors of estimation, though small, are not necessarily insignificant.

Uniformity and Diversity: Hippocampus and Olfactory Bulbs

An analysis of the size of the hippocampus in different species is interesting in a different way from that of the more prominent structures. It is, first, a structure that will never be revealed in a fossil endocast, because it is entirely hidden under the mantle of other cortex, and it could be enlightening to determine the extent to which the size of hidden structures can be estimated from gross brain size. Second, the hippocampus may be an unusually important component of the brain in the control of “higher mental processes,” integrating information from other parts of the brain. As mentioned earlier, it is the brain structure most clearly implicated in memory, and yet it is “primitive” cortex rather than neocortex. Finally, the analysis is of a relatively small structure in the brain as estimated from the size of the whole brain, which stretches our notion of “first

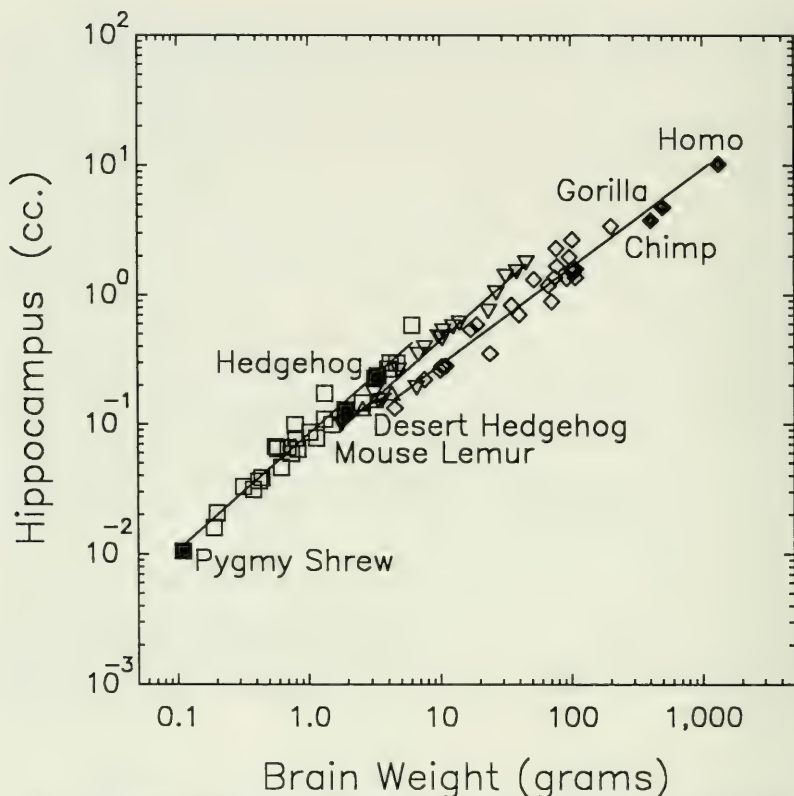


Fig. 11. Hippocampus volume as a function of brain size in 76 species of mammals. Symbols as in fig. 10. Regression equations (assuming errors only in Y) and correlation coefficients: entire sample: $Y = 0.08 X^{0.69}$, $r = 0.980$; insectivores: $Y = 0.08 X^{0.90}$, $r = 0.980$; prosimians: $Y = 0.06 X^{0.90}$, $r = 0.983$; anthropoids: $Y = 0.05 X^{0.76}$, $r = 0.974$. Data from Stephan et al. (1981).

approximations.” The relationship of the size of the hippocampus to total brain size in our sample of 76 species of mammals is graphed in figure 11.

Although not quite as orderly as those seen earlier, the relationship is still an impressive demonstration of the uniformity of the structure of the brain in different species. It is clear that the hippocampus is not unusually large in humans, nor is it unusually small. Stephan et al. reported its volume as 10.3 cc, and the regression equation for anthropoids (coefficients: 0.05000, 0.75753) predicts a volume of

11.6 cc for a primate with a brain of human size. Most significantly, it is clear that the hippocampus is a fairly constant part of the brain in all of the species in our sample.

Other hidden brain structures, such as basal ganglia, provide more impressive evidence of the uniformities of brain structure across species. I chose to show hippocampus, because its place in the architecture of the brain is important for my analysis of the evolution of language. For that I will make old-fashioned statements about "olfactory brain," putting hippocampus in that category ("rhinencephalon") to help us think about olfaction in a particular evolutionary and behavioral context.

The second part of the morphometric analysis in this section is on the olfactory bulbs. I present it in connection with my view on language, and, incidentally, as an almost unique example of diversity of organization. Differences in the size of the olfactory bulbs are the best example that I can find of important differences in mammalian brain structures that are visible on endocasts, and you can think of the next graph as a relief from the dreary uniformity that we have encountered thus far. The results are pleasingly chaotic, but not too hard to analyze. The data are mainly from Stephan et al. (1981) as in the previous illustrations, but since I will also be concerned with olfaction in carnivores for my analysis of the origins of language, I have added a few points that I had determined on the endocasts of six carnivores (Jerison, 1973: table 11.3). The full data set is in figure 12.

The outstanding features of the graph are, first, the unusual decrease in relative size of the olfactory bulbs in anthropoids, and second, the appropriateness of the insectivore regression for characterizing carnivore data. Insectivores seem to represent a mammalian norm in olfactory capacities, and the primate condition should evidently be viewed as a specialized adaptation involving reduced olfactory representation and function. I have no explanation for this primate specialization, but the fossil record of the brain as revealed in endocasts is that olfaction was already reduced in Miocene anthropoids, more than 15 mya, but not in the one Oligocene anthropoid endocast that is known. Reduced olfactory bulbs appear to be a primitive shared trait for the living species of monkeys, apes, and

Homo sapiens. Living humans are unusually poorly endowed in this regard, even when compared with most other living anthropoids.

In our evolutionary history as anthropoids, although the olfactory bulbs became much reduced, the hippocampus evidently remained relatively normal in size. Having normal hippocampus but reduced olfactory bulbs implies a differentiation of “olfactory” functions, in which information from the external world, mediated by the olfactory bulbs, is attenuated, although further processing of *that kind of information* by the more central structure, that is, the hippocampus, remains normal. For my speculations on the origin of language, the central issue is on the kind of information that the earliest hominids needed for their way of life and the extent to which it was of the type that normally involved a significant olfactory dimension for information about the external world.

Uniformity and Diversity in Brain Organization: Conclusions

With the exception of the relative size of the olfactory bulbs, the brain's gross structural organization appears to be remarkably uniform across species of mammals. In analyzing organization, however, the problem is to avoid mistaking these uniformities for identities. It evidently requires relatively small changes in the quantitative measurements that I have reported to support major differences among species in neural control. This must be the case, because there are major differences in behavior patterns among all of the species that provided the data for this section. There must be correlated differences in their nervous systems, which are not detected in my analysis. Since this is the kind of analysis that can be applied to fossil data, it is clear that many behavioral differences will simply not be available for analysis from the data on fossil brains. But do not despair. In the next section I will describe a class of differences, measured as “encephalization,” which are eminently analyzable.

The uniformities appear as first approximations in our analysis, and we should appreciate the differences among levels of approximation. For example, according to our data (fig. 9), the first approximation represented by fitting a single straight line to the data implies that the forebrain fraction of the brain increases as the brain

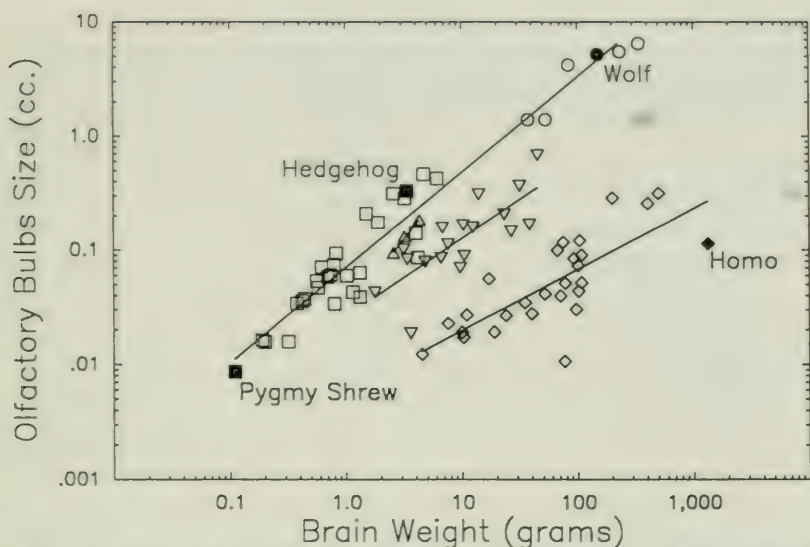


Fig. 12. Volume of the olfactory bulb as a function of brain size in 82 species of mammals. (O), Carnivores; other symbols as in fig. 10. Some statistics: insectivore regression: $Y = 0.07 X^{0.91}$, $r = 0.903$; combined insectivore + carnivore regression: $Y = 0.07 X^{0.84}$, $r = 0.971$. Correlations, all data, $r = 0.291$; prosimians $r = 0.783$; anthropoids $r = 0.768$. Data from Jerison (1973) and Stephan et al. (1981).

becomes larger (the meaning of the exponent of $1.07 > 1.00$). It is only with the help of a more detailed analysis, performed separately on different groups of species, that we recognize that the first approximation is probably misleading. The fundamental fact that underlies the approximation appears to be that within particular groups of species, the forebrain is a fixed fraction of the brain size, but the fraction happens to be largest in our larger-brained primate species (Anthropoidea), intermediate in our smaller brained primates (Prosimiae), and smallest in our very small brained insectivore species. Fitting a single line to our entire sample results in a steeper slope "between-groups" than is present within each of the subsamples.

To suggest a comprehensive view of these relationships, I present a multivariate analysis, a "principal components" factor analysis of 12 morphological variables (logarithmic data) listed in table 1. The data are on the same 76 species from Stephan et al. (1981). The factor analysis was performed with the factor program in SYSTAT (Wilkinson, 1989).

TABLE 1
Factor Loadings and Percent Variance Explained by Two Principal Components (Factors) in Brain and Body in 76 Species of Mammals

	Factor 1	Factor 2
	(General brain size)	(Olfactory bulbs)
Neocortex	0.991	0.059
Total brain weight	0.989	0.137
Diencephalon	0.987	0.144
Basal ganglia	0.987	0.133
Cerebellum	0.983	0.168
Mesencephalon	0.972	0.196
Medulla	0.966	0.224
Hippocampus	0.962	0.239
Schizocortex	0.954	0.274
Body weight	0.939	0.285
Piriform lobe	0.899	0.399
Olfactory bulbs	0.157	0.985
Percent total variance	85.855	12.668

Note: Varimax rotation. Data from Stephan et al. (1981).

Although this is stretching the analysis a bit, I will discuss the factors in table 1 as if they were fundamental causal variables, which are represented to different extents in the brains of the different species. From this perspective, almost all of the variance (98.5 percent) in the data summarized in table 1 is "explained" by just two factors. The first of these, accounting for 85.8 percent of the variance, can be described as a general brain size factor. It is represented most strongly in the amount of neocortex, but almost as strongly in total brain weight. It is a "general" factor in the sense that it is strongly represented in all of the brain structures, with the exception of the olfactory bulbs, and also in body weight. This corresponds to the general impression from the analyses in the previous sections that the parts of the brain hang together rather well, and when one part is enlarged the rest of the brain tends to be enlarged as well.

The second factor, accounting for 12.7 percent of the variance, is an olfactory bulb factor. It is represented primarily by the olfactory bulbs, with a modest representation in the parts of the brain that are classic "rhinencephalon" (piriform lobes, schizocortex, and hippocampus) and in body weight.

We can think quantitatively about each of the structures by asking what fraction of their variance is accounted for by each factor. The fraction is the square of the factor loading. Thus factor 1 accounted for 98.2 percent of the variance (0.991^2) in neocortex across the 76 species, and factor 2 accounted for essentially none (0.3 percent). The remaining 1.5 percent of neocortex variance is in residual factors, which we may think of as error factors. Factor 1 accounted for 79 percent or more of the variance in the other brain structures, with the exception of the olfactory bulbs (2.5 percent). Factor 2 accounted for 97 percent of the variance in olfactory bulbs, hence my naming it an olfactory bulb factor. This factor accounted for between 5.7 and 15.9 percent of the variance in the other rhinencephalic structures.

The general conclusion about the organization of the brain is that it is orderly enough to justify the use of gross brain size as a kind of statistic to estimate the sizes of other parts of the brain, excepting only the olfactory bulbs. We have seen from figure 4, and the discussion of uniformity in the corpus callosum and elsewhere, that brain size estimates the total information processing capacity of the brain in a species. Its efficiency as a statistic for estimating the size of the parts of the brain implies that the partitioning of processing capacity is relatively uniform in different species. Brain size, thus, estimates both processing capacity and the organization of processing capacity. Small (residual) departures from estimated capacity can be significant. Nevertheless, as a first approximation, it is clearly the case that if we know how large a mammalian brain is we know its processing capacity and can make reasonable guesses about its organization.

ALLOMETRY AND ENCEPHALIZATION

The analysis that I just discussed tells us what to expect of a brain if we know its size. The analysis that I present now is of brain-body relations. It tells us in a very general way why brains are as large as they are. It also provides a statistical knife, as it were, for dissecting the brain. The "cut" is into two components, distinguished conceptually but not anatomically (Jerison, 1977, 1985a). One component

may be thought of as involved primarily in the control of general bodily functions (an allometric component from brain-body allometry). The second can be identified with higher mental processes, or mind—or at the very least with neural control not related to body size (an encephalization component). Such an analysis of brain-body relations provides a quantitative framework that can be applied to the fossil evidence on the evolution of the brain.

The main factor determining brain size in mammalian species is body size, and an allometric equation describes this basic relationship. Deviations from allometry represent degrees of encephalization. The usual modern approach to allometry is to fit a straight line to the logarithms of body and brain sizes in a sample of species. The equation of the line is the brain-body allometric equation. The most common measure of encephalization, the “encephalization quotient” EQ (Jerison, 1973), is the ratio of actual brain size to expected brain size when expected brain size is estimated by the allometric equation. In statistical language, the quotient is a “residual” computed from the regression of log brain size on log body size. In large samples of mammalian species, about 90 percent of the variance in brain size is “explained” by body size and about 10 percent by encephalization. The analysis is “between-species.” Encephalization is a character of a species; it is usually meaningless to discuss differences within a species in encephalization.

Allometry and encephalization do not have to be defined by regression equations or residuals, but most of the recent work on brain evolution involving brain-body allometry uses this approach, which might be called “parametric,” since it involves the estimation of the parameters of a normal probability distribution. Although I rely on a nonparametric analysis in much of my evolutionary analysis, I will begin with an analysis and critique of this parametric quantification (cf., Deacon, 1990; Harvey, 1988; Hofman, 1989; Martin, 1983; Pagel and Harvey, 1988, 1989), because it is the source of many insights, a few problems, and some interesting controversy. As in the last graphs, I begin with data from Stephan et al. (1981).

The work by Stephan’s group is especially relevant for evolutionary analysis because of the species they used. They worked with insectivores to represent a primitive grade of brain evolution and

to provide an evolutionary perspective on the human brain. We now recognize that the issues are more complex (Cracraft and Eldredge, 1979; Patterson, 1987), but insectivores appear to be a reasonable if not ideal model for the base group from which most placental species evolved (Johnson et al., 1982). They resemble the earliest mammals both skeletally (Savage and Long, 1986) and in their endocasts (Jerison, 1990; Kielan-Jaworowska, 1986). Although primates are presently a highly encephalized order of mammals, they are also a very ancient order, probably derived during the late Cretaceous period from a species comparable to living insectivores or tree shrews. Comparisons between insectivores and primates are, thus, very appropriate for our topic.

Allometry and Encephalization in Insectivores and Primates

The quantification of encephalization in insectivores and primates is summarized in figure 13A–D. In contrast with the previous graphs, brain size is now treated as the dependent variable, and body size is the independent variable. The four graphs present the same data, fitted in different ways, to illustrate several parametric approaches. As in most of the previous graphs, the fits by regression analysis shown in figures 13A and 13B are remarkably good. The separate fits to insectivores and the two groups of primates and the fit to the entire sample of 76 species are equally good, all supported by correlations of at least 0.96. It is also clear by inspection that the three species of tree shrews are at a prosimian rather than insectivore grade of encephalization; elephant shrews are at an insectivore grade.

The fact of encephalization is evident in the vertical displacement of the lines that are fitted to the three groups (figure 13A), but we cannot compare the groups quantitatively, because both the slopes and intercepts are different, although, again by inspection, we can recognize the qualitative difference. Fitting a single line to all of the data (figure 13B) is faulty for the same reason as in figure 9; the slope of 0.91 is an obvious artifact of small body size in the sample of small-brained insectivores and larger body size in the sample of large-brained anthropoids.

For quantitative comparisons of the groups, we can force the lines

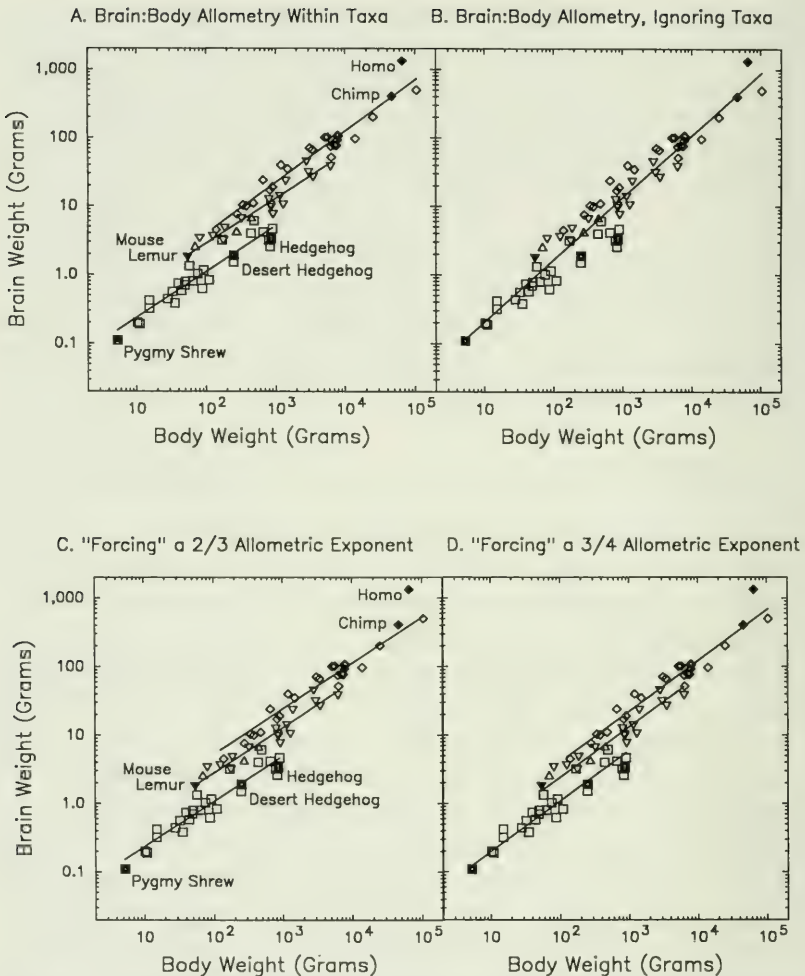


Fig. 13. Brain size as a function of body size in 76 species of mammals, symbols as in fig. 10. Data from Stephan et al. (1981). The graphs indicate several different ways of describing the data with regression equations. Fitted regression equations (assuming errors only in Y) and correlation coefficients for the separate taxa (fig. 13A): insectivores: $Y = 0.05 X^{0.67}$, $r = 0.946$; prosimians: $Y = 0.14 X^{0.66}$, $r = 0.960$; anthropoids: $Y = 0.13 X^{0.75}$, $r = 0.972$. For the entire sample, lumping the taxa (fig. 13B): $Y = 0.05 X^{0.91}$, $r = 0.966$. "Forced" regressions (figs. 13C and 13D) are drawn through the centroids of the taxa, with exponents (slopes) of 2/3 and 3/4. At 2/3, intercepts (proportional to EQ) are 0.05, 0.06, 0.12, 0.13, and 0.24 for insectivores, water shrews, tree shrews, prosimians, and anthropoids, respectively. At 3/4, intercepts are 0.03, 0.04, 0.077, 0.074, and 0.12. The effect on EQ estimates is trivial.

to have equal slopes (exponents), and I show this in figures 13C and 13D, in which parallel lines are drawn through the centroids (geometric means) of each group. The lines are at slopes of $2/3$ and $3/4$, the slopes that have been discussed and analyzed during the past two decades.

Let me first contrast these results with those of figure 9, above, in which the same groups were compared with respect to the amount of forebrain per unit brain size. In that illustration we saw that the forebrain becomes a somewhat larger fraction of the brain in the insectivore-prosimian-anthropoid "progression," with an increase of about 10 percent per grade. In the graphs of figure 13, we can see an approximate doubling in relative brain size (encephalization) in the same series. Figure 13 shows that the available amount of information processing capacity per unit body size increased; figure 9 shows how that increase affected the way in which information processing capacity was organized. There was reorganization by changing the "investment" in capacity handled by forebrain as opposed to the rest of the brain. Investing in forebrain is not necessarily a more efficient way to handle information, although it implies an increased investment in "higher" functions that are typically fore-brain functions.

The quantitative relations show that only a relatively small part of the additional capacity was invested in the forebrain and in the functions that it controls. (Doubling brain size corresponded to only a 10 percent rise in forebrain size.) At a given size, whether determined by allometry or encephalization, the brain tends to be organized in the same way. To illustrate, I will compare an insectivore and a prosimian that have brains similar in size. Our 250 g desert hedgehog (*Hemiechinus*) had a 1.9 g brain. If the 54 g mouse lemur (*Microcebus*) were an insectivore rather than a prosimian, we would expect its brain to weigh only 0.7 g, but, in fact its brain weighed 1.8 g. In this case our primate was a bit more than twice as encephalized as an insectivore of its body size. Is the fact that brain size in the desert hedgehog is explained by allometry and in the lemur by encephalization reflected in the organization of their brains with respect to the size of the forebrain? The actual volume of the desert hedgehog's forebrain was 1.22 cc; the mouse lemur's forebrain was

1.20 cc. This is an example of how little it can matter for a brain's organization whether its size was determined by the allometric correlation with body size or was a result of encephalization.

The Allometric Exponent

We have seen in figure 13 that to compare species or groups of species with respect to encephalization we must specify a single exponent for the allometric equation. On log-log coordinates that exponent is a slope, and we must use the same slope for all the subsets to obtain a set of parallel lines that are separated by amounts of encephalization. There has been a good deal of discussion in recent years about the correct value for the exponent (e.g., Hofman, 1989; Martin, 1983), which rejects the $2/3$ exponent used for many years (Snell, 1891; von Bonin, 1937; Jerison, 1973), and accepts instead a value of $3/4$, determined empirically by regression analysis on large samples of mammals (Eisenberg, 1981; Martin, 1981). In most instances the choice of $2/3$ or $3/4$ has very little effect on the analysis of encephalization, and this is illustrated in the relations between the "forced" intercepts in figure 13. The groups differ by about a factor of about 2 with either exponent.

The choice of exponent is important primarily for theoretical analysis. If the exponent is $3/4$, an implied surface-volume relationship that can be related to the brain's function in mapping may not be supported. Mapping involves converting information about volumes into information about surfaces, and the $2/3$ exponent has a place in such conversions (Jerison, 1977). There is no theoretical explanation for a $3/4$ exponent, but that is the empirical allometric exponent in the function that relates basal metabolic rate to body size (Kleiber, 1947). This suggests a metabolic determinant of brain size in mammals, although that is subject to other criticisms (McNab and Eisenberg, 1989).

There is a clue in the graphs in figures 9 and 13 on the meaning of a "true" exponent and on a correct way to use exponents for theoretical analyses. If "true" refers to an empirical result for the largest available sample, we would have concluded from figure 9 that the true exponent for forebrain-whole brain relations was 1.07.

The evidence from the subsamples, however, seems compelling that an exponent of almost exactly 1.0 represents the situation more correctly. The difference is that with an exponent of 1.07 we would conclude that it makes no difference if the brain is from an insectivore or primate, and that there is a general trend, independent of taxonomy, for larger brains to have somewhat more forebrain than do smaller brains. If we take 1.0 as the true exponent, it means that there is a pattern of brain organization within each taxon such that the forebrain is always a constant fraction of the whole brain. The groups would then be differentiated, and the basis would be (partly) the value of that fraction. We would conclude that insectivores have relatively less forebrain than prosimians and that prosimians have relatively less than anthropoids.

The two possible conclusions from the data of figure 9 can be thought of as hypotheses about factors determining the organization of the brain. There is nothing in figure 9 to suggest that one or the other hypothesis is better, although our insights as biologists may incline us to prefer the exponent of 1.0 because of its simple implications for how the size of the forebrain is determined. The line of reasoning is that a fixed-fraction adaptation is part of the mammalian bodyplan, and that natural selection conserves that body plan while modifying a growth factor in different groups to change the fate of the forebrain fraction. The modification would be involved in the transformation of an insectivore species into a prosimian and a prosimian species into an anthropoid. Such transformations are consistent with our knowledge of evolutionary history, about the ancestry and relations of these groups.

In the analysis of encephalization in figure 13, we would have to propose an allometric exponent of 0.91 (fig. 13B), were we to take sample size as the criterion for acceptability. As in figure 9, there would be no reason to support exponents of 0.65, 0.66, or 0.75 (the subgroup exponents) as more fundamental on statistical grounds, although they are closer to the consensus about a "true" exponent.

In my view a "true" exponent should be a theoretical value, based on a theory of brain size (see Jerison, 1977), and all empirical exponents should be related to the theoretical value. I continue to support the choice of a value of $2/3$ as a didactic device to emphasize

TABLE 2

Factor Loadings and Percent Variance Explained for Brain and Body by Three Principal Components (Factors) in 76 Species of Mammals (in Order of Loading on Factor 3)

	Factor 1	Factor 2	Factor 3
	(Allometric size)	(Olfactory bulbs)	(Encephalization)
EQ (re 2/3 exponent)	0.540	-0.084	0.837
Total brain weight	0.919	0.129	0.369
Neocortex	0.922	0.051	0.366
Basal ganglia	0.924	0.124	0.349
Cerebellum	0.922	0.157	0.346
Piriform lobe	0.836	0.394	0.343
Diencephalon	0.931	0.132	0.330
Mesencephalon	0.918	0.185	0.326
Hippocampus	0.920	0.224	0.294
Schizocortex	0.912	0.259	0.294
Medulla	0.932	0.206	0.276
Total body weight	0.925	0.261	0.217
Olfactory bulbs	0.196	0.978	-0.042
Percent total variance	73.391	11.207	14.173

Note: Varimax rotation. Data from Stephan et al. (1981).

mapping. It can be shown that if 2/3 is fundamental, empirical values such as 3/4 should be found in empirical analyses of large samples of mammals (Jerison, 1985b), but this is not necessarily the best value to use for the analysis of encephalization. The issue is related to the evolution of mind only because the quantitative estimation of encephalization is as a residual relative to an allometric estimation of expected brain size, and for that estimation the only real requirement is that a single exponent be used, because otherwise a residual would be meaningless.

Encephalization Quotients

To present the relationship between encephalization and the component structures of the brain I performed a multivariate analysis of the same kind as in table 1, but added an encephalization quotient to the variates in the analysis. Encephalization in a species was measured as its typical brain size divided by the term, $0.12 P^{2/3}$,

where P is body size in grams. The results, using an exponent of $2/3$ for computing all EQs, are summarized in table 2. (Essentially the same results are obtained with a $3/4$ exponent and a multiplier of 0.055.)

We must keep in mind that EQ is a residual, and the correlation coefficient, $r = 0.966$, between log brain and log body size in our sample of 76 species (fig. 13) indicates that EQ would account for less than 8 percent of the variance in brain size if it were taken with respect to the "best-fitting" slope of 0.91. It accounts for a bit more when the residuals are with respect to the slope of $2/3$, but most of the variance would still be attributed to the allometric effect, that is, the correlation with body size. From table 1 we might, therefore, have guessed that about 10 percent of the general brain size variance and 10 percent of the olfactory bulb variance would be partitioned out when we removed the "residual" variance of encephalization. Table 2 shows that the encephalization variance was created only from the general brain size component of table 1. The 86 percent of variance analyzed in table 1 as related to brain size is reduced to 73 percent in table 2, with 14 percent of the variance associated with encephalization. It is appropriate, therefore, to call the first factor an allometric size factor, which would represent the allometric component of brain size. Note that the loadings for brain size and body size are almost identical, as one would expect for such a factor.

The fraction of variance identified with the olfactory bulbs remained about the same at a bit over 10 percent, and was independent of encephalization and of allometry. We could have anticipated this from the appearance of figure 12; it should be interpreted primarily as reflecting our unusual sample of species, in which the size of the olfactory bulbs was determined more by taxonomic status than anything else, because of the heavy sampling of anthropoids. Had we used more "normal" orders of mammals (e.g., carnivores and ungulates), it is likely that the olfactory bulbs would have had a significant loading on the allometric size factor. But in no case would we expect the size of the olfactory bulbs to be related to encephalization (Jerison, 1990).

Uniformity of organization is evident in table 2 in the similar pattern of loadings for the brain structures (not EQ) on both factors

1 and 3. The effect of encephalization was similar for all of the parts of the brain with the exception of the olfactory bulbs. It is represented most strongly in the measure of neocortex (as expected), but it is represented in every other part of the brain proper. The result also indicates that bivariate graphs involving either brain or body on the abscissa and a part of the brain other than the olfactory bulbs on the ordinate will resemble figure 9. More can be said about multivariate analysis, but that can be left for another occasion.

EVOLUTION OF ENCEPHALIZATION

When species differ in brain size and are similar in body size, we define the difference as encephalization. Since encephalization is a fraction of gross brain size, it represents the fraction of processing capacity that is not determined by body size. Although I have not developed the theory here (see Jerison, 1977; 1985b), most differences in encephalization should be attributed to differences in the extent of mapping in the brain.

We can recognize encephalization in graphs of brain and body data that present clouds of points of brain and body sizes in different species (see fig. 14). We do not really need the regression lines in figure 13 to recognize anthropoids as more encephalized than prosimians and both primate suborders as more encephalized than insectivores. The analysis of encephalization can be pictorial and not numerical.

My remaining analysis does not depend on computed regression coefficients or encephalization quotients. I rely on graphic rather than numerical methods to summarize the data. It is possible to compute the numbers, but I prefer not to, because an array of numbers implies precise knowledge that is not really available for these data. I will graph the patterns of encephalization in living vertebrates, and the graphs will be the background against which to view the fossil evidence on the evolution of the brain.

With the exception of human data, each of the 200 or so points in figure 14 represents a single living species; the data are from Quiring (1950) and the graph is from my book (Jerison, 1973). The human data are on 42 men and the entire range is framed by the

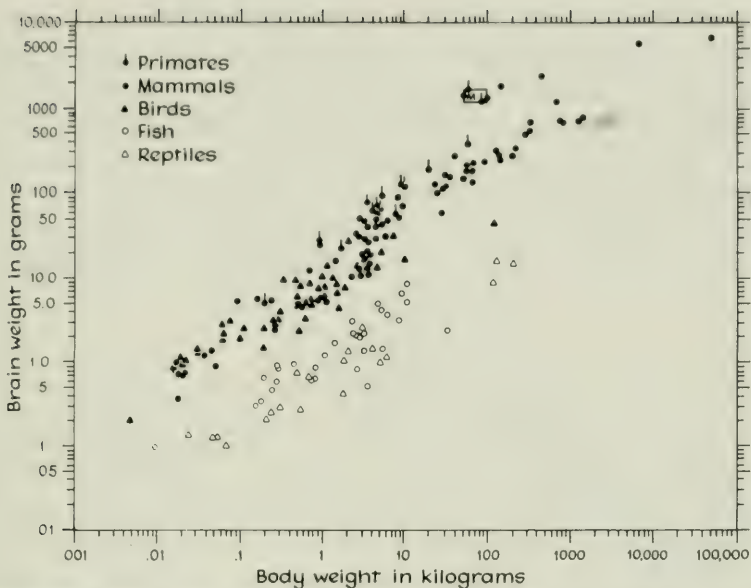


Fig. 14. Brain weights and body weights in 198 species of vertebrates, graphed on logarithmic coordinates. (Data from Quiring, 1950, graph from Jerison, 1973, reprinted by permission)

rectangle marked M. As you can see, the variability within our species, notorious as it is reputed to be, is small and unimpressive when seen against the background of the other data. The size of the data points in other species can represent within-species variability.

There are two outstanding regularities in the graph. The first is the angular orientation of the clouds of points for the classes of vertebrates, which is the graphic representation of brain-body allometry. The second effect is the separation of the clouds of points of birds and mammals on the one hand and of reptiles and bony fish on the other. That vertical separation represents encephalization. Allometry and encephalization are thus represented graphically, without further “parametric” or numerical analysis.

The size of brain and body of each species graphed in figure 14 can be thought of as a response by natural selection to the diversity of the environmental niches to which species became adapted. A graphed point would be a qualitative measure of the response, and

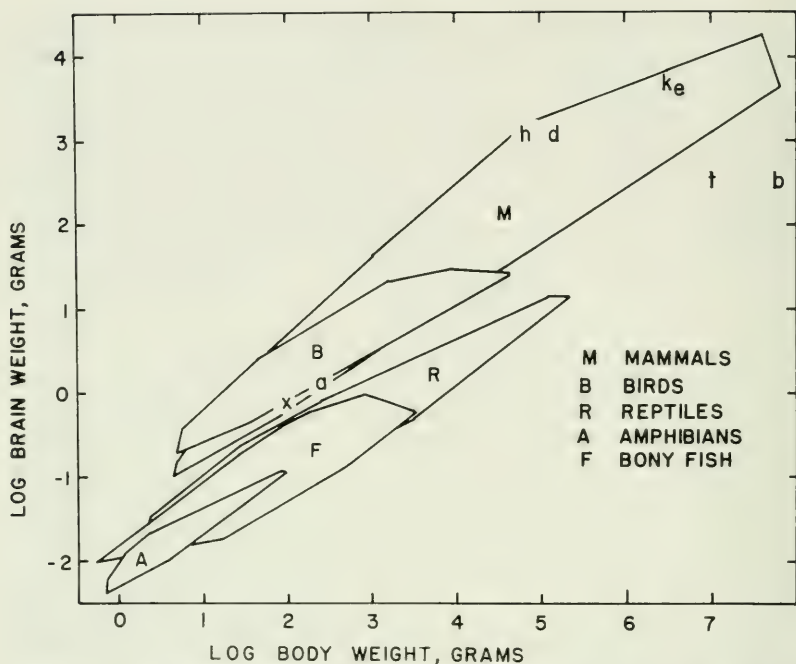


Fig. 15. Brain-body relations in 623 living vertebrate species enclosed in minimum convex polygons. The samples are 309 mammals, 180 birds, 46 bony fish, 40 amphibians, and 48 reptiles. Additional data are: **d**, *Tursiops truncatus* (bottle nose dolphin); **e**, elephant; **h**, humans; **k**, *Orcinus orca* (killer whale), two dinosaurs (**t**, *Tyrannosaurus*, **b**, *Brachiosaurus*); **x**, the 150-million year old mammal, *Triconodon*, and **a**, the early bird, *Archaeopteryx*. (From Jerison, 1987, reprinted by permission)

the regions in this adaptive “brain-body space” occupied by each class of vertebrates represents the range of responses to evolutionary opportunities that have taken place in that group. We may visualize these effects most clearly, without curve-fitting, by drawing convex polygons about appropriate sets of points. I present such polygons in figure 15 from a larger data set (Jerison, 1987).

The polygons in figure 15 are regions in brain-body “space,” and they describe regions of realized evolutionary opportunities at the present time. All living mammals are within the mammalian polygon, birds within the bird polygon, and so on. To anticipate the addition of a time dimension to this evolutionary view, I have added points representing fossil species: two dinosaurs, *Tyrannosaurus* and

Brachiosaurus, the earliest bird, *Archaeopteryx*, and the earliest mammal on which we have evidence of the brain, the upper Jurassic *Triconodon*. I have also indicated some well-known living mammalian points: humans, dolphins, killer whales, and elephants. As you may guess, the largest and smallest birds in the sample are an ostrich and a hummingbird. The largest mammal is a blue whale, and the smallest is the pygmy shrew. I will now consider some of the fossil evidence on the evolution of the brain in the context of these polygons.

Dinosaur Brains

To illustrate the data and the very simple method, I begin with the always fascinating dinosaurs, and I analyze their evolution as a problem in brain evolution. The essence of the analysis was in figure 15, in the minimum convex polygon that enclosed the available data on living reptiles and the two points added for *Tyrannosaurus* and *Brachiosaurus*. The scientific issue is: Did dinosaurs become extinct because of their small ("walnut-sized") brains? This old saw of popular science can be analyzed by first answering a related question: Did dinosaurs have small brains? I had asked a similar question at the beginning of this lecture, about the 35 million year old fossil mammal, *Bathysynaps reevesi*, and answered by comparing the brain of *Bathysynaps* with that of living domestic cats, which were probably about the same body size. The answer for *Bathysynaps* was "Yes, it was small-brained, at least when compared with cats." The problem with dinosaurs is that there are no living reptiles in the size range of those graphed in figure 15, and we have to control for body size by performing an allometric analysis. But we do not need a regression analysis. It will be enough to use the allometry evident in the orientation of the convex polygons.

We answer by examining the appearance of reptile polygons with and without dinosaurs. Hopson (1977) published the polygons of figure 16. He showed the effect of adding dinosaur data to the polygon for living reptiles; we can ignore the "regression line" at slope $2/3$ through that polygon. As you can see, adding dinosaurs extended the living reptile polygon to include larger body sizes but did not

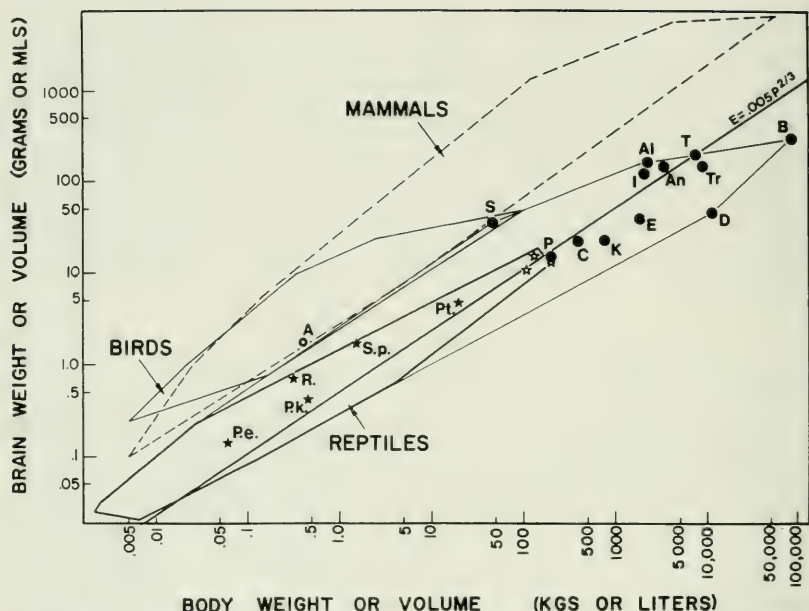


Fig. 16. Fossil reptile data added to mammalian, avian, and reptilian brain-body polygons. (A., *Archaeopteryx*, the earliest bird.)

Pterosaurs (★): P.e., *Pterodactylus elegans*; P.k., *Pterodactylus kochi*; Pt., *Pteranodon* sp.; R., *Rhamphorynchus*; S.p., *Scaphognathus purdoni*.

Dinosaurs (●): Carnosaurs: Al, *Allosaurus*; T, *Tyrannosaurus*. Coelosaur: S, *Stenonychosaurus*. Sauropods: B, *Brachiosaurus*; D, *Diplodocus*. Ornithopods: An, *Anatosaurus*, C, *Camptosaurus*, I, *Iguanodon*. Ankylosaur: E, *Euplocephalus*. Stegosaur: K, *Kentrosaurus*. Ceratopsians: P, *Protoceratops*, T, *Triceratops*. (From Hopson, 1977, reprinted by permission)

affect its orientation, and it altered its shape only slightly. The lower brain-size margin of the reptilian polygon remained the same, but its upper limits became somewhat higher, reaching the lower avian and mammalian limits. This is attributable to the recently reported datum on the ostrich-like dinosaur *Stenonychosaurus* (Russell, 1972), which appears to have been comparable in brain and body size to living ostriches.

With this simple procedure we have our answers: Dinosaurs were at least normal reptiles with respect to brain size. If they were distinguished in this respect, it was that some species had evolved unusually *large* brains, and these species were at a low avian, almost

mammalian, grade of encephalization. Since much less encephalized reptiles survive, we answer our main question: We cannot attribute the dinosaurs' extinctions to their "walnut-sized" brains. We have not asked, but we can nevertheless add: since dinosaurs were reptiles, from a mammal's perspective dinosaur brains were small, but the brains of the great thunder lizards were not walnut-sized. The *Tyrannosaurus* brain probably weighed a pound and a half—comparable to a walnut's weight only if walnuts were made of uranium. A grapefruit would be a better model for its size.

Early Encephalization: Sharks, and Mesozoic Birds and Mammals

Most fish are known only as flattened fossils in which the endocasts cannot be properly analyzed for size. The only good fossil endocasts from bony fish are from very small unflattened specimens, and these are strikingly similar to those of living species in both size and shape and lie within the same convex polygon (fig. 15) as living fish. Perhaps surprisingly, the earliest "experiment" with enlarged brains seems to have occurred in supposedly primitive cartilaginous fish, according to evidence on Paleozoic (about 300 mya) sharks. The species *Cobelodus aculeatus* is a relatively uncrushed fossil, and Zangerl and Case (1976) compared its endocast with that of the living horned shark (*Heterodontus*). Although the fossil's endocast has not been measured (its body was about 80 cm long), both its brain and body appear to have been similar in size to those of the horned shark, which would put them above the highest grade of encephalization of living bony fish (Ebbesson and Northcutt, 1976) and above that of any other fossil vertebrate of their time.

It was not clear to me from examining Zangerl and Case's illustrations that the *Cobelodus* brain was organized in ways radically different from that of the horned shark, but Zangerl and Case believe that the fossil's brain was more enlarged in the cerebellar area and less in the forebrain area. Brain organization at this gross level is significantly more variable in fish than in birds or mammals, and it is impossible to suggest a proper interpretation of such a difference, even if it is present. Processing capacity by the entire brain of *Cob-*

elodus was almost certainly high compared to living bony fish. *Cob-elodus* probably represented an advance in encephalization. In a cladistic analysis of the relationships among living sharks, Northcutt (1989) indicated that the earliest sharks were likely to have been smaller-brained and comparable to bony fish. The evidence of *Cob-elodus* indicates that at least one group of early sharks may have become more encephalized.

The evidence on encephalization in birds is clearer. There is no question that they were more encephalized than their reptilian ancestors. Two endocasts are known for the earliest bird, *Archaeopteryx*, which lived about 150 mya. The better known one is at the British Museum (Natural History). From my reconstruction (Jerison, 1973; cf. Whetstone, 1983) I estimated its endocast volume as 0.9 cc and body weight as between 250 and 500 g, with the latter as a maximum. Hopson estimated the endocast as twice as large, and body size toward the lower end (about 300 g). The *Archaeopteryx* point in figure 15 is my estimate and slightly below the lower avian boundary but above the upper edge of living reptiles. Hopson estimated it (fig. 16) as clearly within the range of living birds. His estimate incorporates suggestions from the newer data on the second *Archaeopteryx* with known endocast, the Eichstätt specimen (Wellnhofer, 1974). Although I am not yet satisfied about whether my older estimate or Hopson's newer one is correct, both estimates agree in placing *Archaeopteryx* above the grade of encephalization achieved by any reptiles in that body size range. The much larger ostrichlike dinosaurs, mentioned earlier, may also have been in the avian range of encephalization.

The earliest evidence on the mammalian brain, on the upper Jurassic *Triconodon mordax*, indicates that this mammal species was about four times as encephalized as a reptile of its body size and that it was in the range of encephalization of living opossums and hedgehogs (Jerison, 1973; cf. Crompton et al., 1978). Later Mesozoic mammalian endocasts (Kielan-Jaworowska, 1986) are at that grade or higher, and it seems to be true that the lowest grade of encephalization in living mammals has always been a minimum for the mammalian bodyplan. Although no Mesozoic mammals seemed to depart very much from that minimum, all Mesozoic

mammals, like all later mammals, were more encephalized than any reptile.

Although the fossil evidence of the mammalian brain is of the same vintage as that of birds, mammals probably preceded birds in the history of life by about 50 million years. (Endocasts are less common than jaws and teeth in the fossil record, and the evidence on mammalian origins is mainly mandibular and dental.) When I first reviewed the evidence (Jerison, 1973), the immediate ancestors of the mammals among the mammallike reptiles seemed to me at a reptilian grade of encephalization. There is new information on mammallike reptile endocasts (Kemp, 1979, 1982; Quiroga, 1980; cf., Jerison, 1985, 1990), which suggests that a mammalian grade was reached by at least some mammallike reptiles. The advance must have occurred at some time during the transition from reptiles to mammals, of course, and it may have occurred in more than one mammallike reptile lineage. We are certain only that it occurred in the lineage of the true mammals, and we know that it had already appeared 150 mya.

I am concerned primarily with mammalian encephalization, and the evidence on Mesozoic mammals is impressive on two major points. From at least 150 mya to the end of the Mesozoic, about 65 mya, there was no obvious or important mammalian encephalization beyond the advance from a reptilian to a minimal mammalian grade. Despite their adaptive radiation into many niches, Mesozoic mammals were similar to one another in relative brain size. I should add that they were all small-bodied compared to living mammals, never larger than domestic cats and much smaller than almost all of their contemporaries among the ruling reptiles of the Mesozoic. Their body sizes are important for our understanding of the selection pressures on mammalian evolution during the Mesozoic and for the origin of "mind" in mammals.

The second major point is that there are many living mammals that are no more encephalized than the earliest on which we have evidence, and some are spectacularly successful in their niches. The Virginia opossum and the European hedgehog are outstanding examples, familiar from the remains of their encounters with automobiles on American and European highways, which provide grue-

some evidence of their evolutionary fitness. Their fecundity must be impressive for them to contribute so significantly to the population of road kills.

Mammalian adaptations can be successful without expansion of the brain beyond the grade established 150 (or 200) mya. After the initial advance from a reptilian grade, there was a remarkable stasis in the evolution of encephalization in mammals in all species until the end of the Mesozoic, which has continued in some species to our own time.

Encephalization in Tertiary Mammals

With the extinction of almost all large land vertebrates at the end of the Mesozoic, about 65 mya, there followed an exuberant adaptive radiation of mammals. Within the first few million years of the Tertiary many large-bodied species appeared, and by the middle Paleocene, species of archaic ungulates as large as living rhinos (the pantodont *Titanoides*) had appeared. (Species are "archaic" if they are members of orders that are entirely extinct. The designation is objective and not evaluative.)

With the exception of the earliest primates that had appeared, brain size in the early Tertiary was determined entirely by allometric factors, and encephalization did not increase. For example, one of the largest of the archaic ungulates, the late Eocene uintathere *Tetheopsis ingens* weighed about 2000 kg, and its endocast was approximate 350 cc in volume. If one imagines an average insectivore evolving to such large size, the equations of figure 13 would lead us to expect it to have a much larger brain—over 800 cc. Bauchot (1978) has pointed out that very large species tend to have smaller brains than expected according to the usual allometric analyses, although in this instance the "error" seems unusually large. The least encephalized of living species is probably the Virginia opossum, with a 6 g brain and 4 kg body. Taking it as the model for *Tetheopsis* would lead one to expect the uintathere to have a 380 g brain. The point is that there had been no important encephalization until relatively late in mammalian history. We can imagine the mammalian radiations of the early Tertiary period as having resulted in archaic

species in which the size of the brain was determined entirely by allometric effects—enlarged hedgehogs or opossums, as it were, with respect to encephalization.

Encephalization in most other mammalian orders began somewhat later, during the Eocene and Oligocene, beginning about 50 mya. The pattern is clearest in carnivores and ungulates. For example, in the horse lineage, the earliest known species, the “eohippus” (*Hyracotherium* or *Protorohippus*) of the lower Eocene had a brain that was intermediate in size between one’s expectation from hedgehogs and from average living mammals. By the middle Oligocene, about 30 mya, *Mesohippus* was at the same grade of encephalization as average living mammals. The later horse species have all been average mammals in the same sense, showing no further encephalization. The pattern was similar in the even-toed ungulates, the order Artiodactyla.

Carnivore encephalization is also easily traced. The earliest true carnivores and the archaic carnivore order Creodonta were intermediate in encephalization, but by the end of the Oligocene the true carnivores were at the grade of average living mammals and have remained at that grade. Creodonts were smaller brained on the average, although some creodont species were at an average grade (Jerison, 1973, 1990; cf., Radinsky, 1977a).

The evolution of encephalization in various vertebrate groups is summarized in figure 17: long periods of equilibrium, and where encephalization is evident its probably rapid course in a group. We can note the long stasis in Mesozoic mammals and the persistence of their grade of encephalization in some living species. Advances in grade in the mammals in the Cenozoic, between 65 mya and the present, occurred separately in several groups. The graph is somewhat misleading on this point, because it was constructed by determining mean grades of encephalization for the indicated groups during major intervals, such as the entire Eocene or Oligocene, and it does not represent changes within those intervals or the diversity of encephalization within groups. However, it can be thought of as indicating the amount of selection for brain enlargement taking place during a period, with the representation reflected in the presence of species at a particular grade. For example, we might read the graph

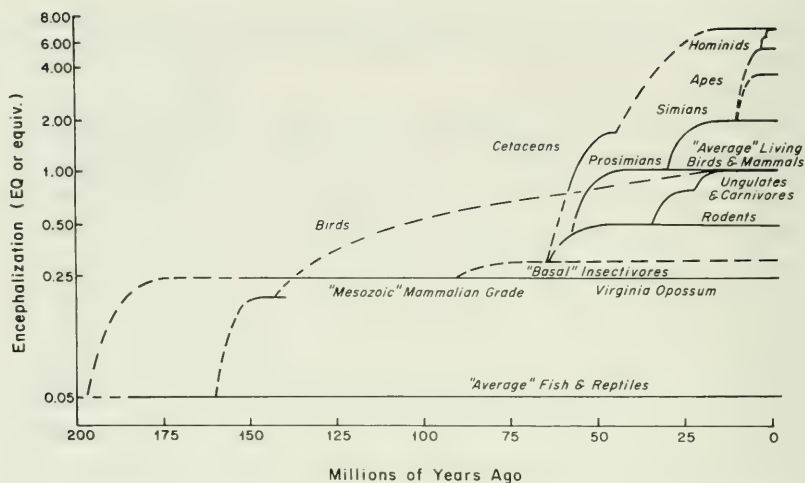


Fig. 17. The time course of encephalization in vertebrates. Encephalization quotients are approximate relative to average living mammals, in which the quotient is defined as 1.0.

on ungulates and carnivores as indicating that during the Oligocene, a successful species had to be approximately 75 percent as encephalized as living ungulates and carnivores. Successful rodents or insectivores were less encephalized then, just as they are now.

Cetaceans and Primates

The highest grades of encephalization among vertebrates have been achieved in cetaceans and primates: in dolphins and hominids, respectively. The history of dolphin encephalization is not known, but from evidence in other cetaceans it seems likely that very impressive encephalization, close to the present highest levels, occurred during the major cetacean adaptive radiations of the Miocene, between 15 and 20 million years ago (Jerison, 1973, 1983).

Although there is some controversy on the primate record (Radinsky, 1977b, 1979; Jerison, 1979; cf., Pickford, 1988), there is little question that early in the Eocene there were significantly encephalized prosimians. The tarsierlike *Tetoni* of the lower Eocene was as encephalized as some living prosimians, although the adapids of the later Eocene were less encephalized: intermediate between an

insectivore and prosimian grade and relatively small brained for primates. Earlier, in the Paleocene, plesiadapids, which are usually considered to be primates, had appeared, and although their endocasts are still unknown, the external configuration of the cranium was rounder; the species appears to have been more encephalized than any of its contemporaries. By the end of the Oligocene, fossil prosimians at about the same grade of encephalization as living lemuroid species had evolved.

The earliest anthropoid primates are known from the late Eocene, and their brains from the middle Oligocene with the appearance of *Aegyptopithecus* (Radinsky, 1979). This early anthropoid was at a prosimian rather than anthropoid grade of encephalization. Encephalization evidently lagged behind skeletal features at that period of primate evolution. The pattern was to be repeated in the hominid lineage (Pickford, 1988).

Hominid encephalization was a much later phenomenon. There is evidence of slight encephalization beyond a great-ape grade in the earliest known hominids, which lived about 3.5 million years ago (Falk, 1987; Tobias, 1981). These were australopithecines and are "hominid" rather than "pongid" for dental and skeletal reasons, not because of enlarged brains. As in the earliest anthropoids, brain evolution appears to have lagged behind other skeletal features.

The major expansion of the hominid brain seems to have begun about 2 mya, with the appearance of *Homo habilis*. Brain size within the range of living humans was achieved within the next million years by the pithecanthropines, *H. erectus*, and it is possible that some increases occurred during its "life" as a species (Falk, 1987). There are technical questions here on the meaning of "species" (Campbell, 1972), but later fossil pithecanthropines may have been bigger brained than earlier ones, suggesting selection for brain size in the "anagenetic" evolution of the species. The general conclusion about the increase in brain size in primates, however, is that encephalization probably lagged behind other events in speciation, which would mean that some primate niches were not initially characterized by selection for brain size, but that encephalization was associated with improved adaptation to those niches.

The fossil record on the hominid brain ends with fossil *Homo*

sapiens. The record here is quite good, and it appears to be true that the neandertals were larger brained than living humans (Kennedy, in press). The earliest *Homo sapiens*, represented by the Swanscombe skull, lived about 250,000 years ago. Differences in brain size among earlier and later populations within the species, however, are not large enough to be interpreted in relation to brain function (Falk, 1987; Holloway, 1981; Kochetkova, 1978). Our best judgment about human brain size is that it reached its present grade with the first appearance of *Homo sapiens*, including the subspecies *H. s. neanderthalensis*.

Hominid species are all in the same body size range, with the exception of the earliest australopithecines, which were somewhat smaller, weighing as little as 20 or 25 kg. Because of the uniformity in body size, differences in brain size represent encephalization. In living humans, within each sex there appears to be no allometric effect at all. There is a sex difference in human brain size (about one standard deviation; male brains average about 125 g heavier than female brains) that is not really understood, but it may be related to body size differences. There are smaller but significant race differences which are also not understood.

The quantitative increases in brain size in hominids (fig. 18) were from somewhat less than 500 cc for the early australopithecines of 2 to 3 mya, rising to a bit over 500 cc (reflecting allometry rather than encephalization) in robust australopithecines of 1.5 to 2 mya. Brain size also rose at that time in *H. habilis*, about 2 mya, to about 750 cc, and then to the range of 800 to 1100 cc in the pithecanthropines, between 1.6 and 0.5 mya. Living and fossil *H. sapiens* (including the neandertals) had endocranial volumes ranging between about 1100 and 1800 cc.

Larger human brains (and cranial cavities) are known, but they and the upper extreme of the living human range—brains weighing more than about 1600 g—may be caused by pathology or postmortem edema (Whitaker, personal commun.). In any case, at the present time there is very little evidence that relates brain size to the quality of mind within the human species, except in cases of microcephaly, hydrocephaly, and senility. Although it is difficult to demonstrate, because of the difficulties of between-species scaling on a dimension

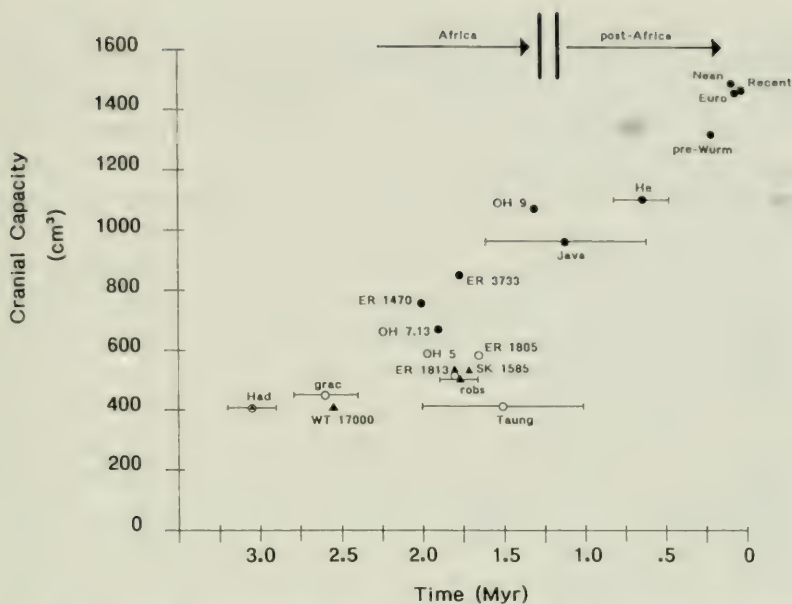


Fig. 18. Mean cranial capacity as a function of time for hominids. (▲), robust australopithecines; (O), gracile australopithecines; (●), genus *Homo*. **Had**, Hadar specimens; **grac**, gracile australopithecines; **robs**, robust australopithecines; for other abbreviations, see Falk, 1987. Horizontal bars indicate time ranges. (From Falk, 1987, reprinted by permission)

of mind (Macphail, 1982), one must interpret between-species differences in encephalization as indicating differences among species in mind or intelligence, whereas normal within-species differences do not have clearly significant behavioral correlates (but see Hahn et al., 1979). This is the case for all vertebrate species including the several hominid species (Jerison, 1985a).

ENCEPHALIZATION AND THE EVOLUTION OF MIND

The graph of the evolution of vertebrate encephalization (fig. 17) points to several critical periods when there were important advances in grade. I will discuss two of these: encephalization at the reptile-mammal boundary, which probably occurred about 200 mya, and hominid encephalization at the transition from a pongid to an australopithecine grade, or from the latter to a *Homo* grade, 2–4 mya.

Since I have published my views on these issues before (Jerison, 1973, 1982a, 1985a,b), I will only outline my analysis of why things went the way they did. But I want to emphasize that in each case there is a real problem in explaining the enormous increases in processing capacity. Remember the data on the mouse. Just half a gram of brain represented 40 million neurons. That is about the amount that would have to be added to the brain of a 100 g reptile to convert it into the brain of a 100 g mammal. The change in the brain would be from about 0.15 g to 0.75 g, both tiny brains, but differing by a factor of five. What could possibly have happened to justify such expansion?

If evolution is parsimonious there must be a justification. We assume that organisms evolve to function efficiently and that they minimize the energy required for their adaptations. As a control system, the brain is profligate in its use of energy. The human brain, which is about 2 percent of the body's mass, is estimated to account for about 20 percent of the body's metabolism. If a job could be done with a minimal amount of neural control, parsimonious evolution would have moved toward such a method rather than toward encephalization, which increases neural control.

The issue is illustrated by vertebrate and invertebrate adaptations for flight. Vertebrate adaptations for flight involve very fine control of muscle systems that are continuously adjusted by the neural machinery. In insects, some of the wing movement is automatically determined by the placement of the wing linkages to the body proper, and aerodynamically appropriate movements are effected by detentlike movements that snap the wing into appropriate successive positions with less elaborate neural control (Wendler, 1983). The insect's system is biologically more efficient than that of vertebrates in the sense that it requires less investment in energetically expensive neural control devices. Encephalization would be expected to occur only if no cheaper way were available to solve an adaptational problem.

Reptiles into Mammals

The explanation for the enlargement of the brain in mammals compared to their ancestors among the reptiles must involve the

perceptual-cognitive domain of information-processing as I discussed this earlier. It is only for such processing that really massive amounts of neural tissue must be available. We, therefore, seek a scenario in which the transition between mammallike reptiles and early mammals involved a species under natural selection for significantly more perceptual-cognitive processing than in normal reptiles.

A reasonably simple and straightforward suggestion is that the selection occurred in species that successfully invaded an adaptive zone of fossorial, crepuscular, and nocturnal niches. We must keep in mind that “normal” reptilian adaptations of Triassic species almost certainly involved primarily visual information about the external world and that a highly efficient eye-brain system had evolved in all reptiles to support such adaptations. These are the systems that still characterize most living reptiles—retinal daylight vision effected and supported by a well integrated retino-tectal and fore-brain system that is efficiently responsive to visual signals. A “reptile” evolving for comparably efficient activity with reduced or absent visual information would require other sources of data about events at a distance.

The special quantitative feature in this problem is that visual processing is done not only in the brain but in the retina of the eye, which is brain tissue that migrated out into the eyeball. The retinal “brain” is very large, and may have millions of neurons. If normal visual processing involves these several million retinal neurons, the same kind of processing with other sense modalities might require that many neurons too. But other systems do not have peripheral brains as part of their structure, so the extra neurons would have to be put inside the head. I have argued that this had to happen, and that the explanation for the first brain enlargement in mammals was as a solution of a packaging problem: where to put the neural machinery that would enable other sensory systems to do the job that is normally accomplished by diurnal vision. The extra half gram of brain may have been just what was needed to do that job.

I have taken the auditory system as my model for replacing the visual system and note that “peripheral” processing in the inner ear region is accomplished by just a few thousand nerve cells in asso-

ciation with the sensory hair cells of the inner ear. Further auditory information processing is accomplished in the brain proper at a bulbar, tectal, and where there is cortex as in mammals, at a cortical level. I have considered the auditory system as having become expanded in early mammals relative to their reptilian ancestors to handle the added information load through the evolution of expanded tectal and novel cortical auditory projections. A comparable argument for the olfactory system would involve, primarily, the expansion of the olfactory bulbs (cf. fig. 12) but also the remainder of the brain's olfactory system. The visual system could also become specialized for nocturnal life, by becoming sensitive to very low levels of illumination, and we can recognize this specialization in mammals in the evolution of the rod system of the retina.

We have to imagine a change from reptile to mammals that was minimal with respect to the requirements for neural control. We should imagine the early mammals as being slightly modified "reptiles" that used unusual sensory systems to navigate their environments the way normal reptiles managed with their visual systems. Their expanded brains were packed with neural machinery that did for other senses what the retino-tectal and associated forebrain system did for the visual information used by diurnal reptiles. Information from these other senses would then be integrated with otherwise reptilian behavior systems for coping with and navigating through their environments, and the information from the novel senses would be used in ways comparable to the ways that the visual system is used by reptiles: providing information about objects and events at a distance.

Most species of mammallike reptiles were evidently replaced in diurnal niches by species of ruling reptiles by the middle of the Mesozoic. Although they were a dominant group at the end of the Paleozoic era, the mammallike reptiles became extinct sometime during the Jurassic period of the Mesozoic era, except for those that, transformed into true mammals, survived and flourished as species of tiny animals (much smaller than any of the reptiles) through the remainder of the Mesozoic. These survivors, numerous and diversified but always small, were the raw material for the exuberant mammalian radiations of the Cenozoic era.

Mind in the Early Mammals?

Consider now the implications of a mammalian adaptation for integrating information received through multiple neurosensory channels about events at a distance. Were the information gathered through a single channel, such as the visual system in reptiles, it might be possible to imagine a tightly coupled arrangement in which visual inputs are associated with motor output to support reflex responses to the changing environment. If the mammalian adaptation is for several sensory modalities to combine to provide the information, different kinds of information would reach different parts of the brain and would have to be assembled and coordinated with the additional message that they provide information about the same features of the external world. How should the sources of information be identified? It would obviously be helpful to label them, regardless of the modality in which they are received and the parts of the brain in which they appear, with labels that identify all of the stimulation with the same environmental source.

The labels would be created by the brain, and they would have to designate “objects” of an external world. There would have to be additional labels for a coordinate system of the external world in which objects would be placed; these would label “space” and “time,” also constructions of the brain. (That the labels would refer to real space and real time in the external world is secondary. The point is that known space and time, as well as *known* objects, must be constructions of the brain.) There would have to be additional properties for the labels, or constructions. They would have to be able to persist over time, and it would have to be possible to store them and retrieve them—to remember them—when needed. The overall activity of labeling amounts to the construction of a real world containing real objects, which is exactly the function of mind as I have discussed it with you.

That the *knowledge* of reality is constructed from sense data seems almost self-evident when information about the external world is coordinated from the combined data of several sense modalities. But this may also be true even when the information appears to be limited to a single modality. We know enough about the complexity

of the visual system, for example, to appreciate that even if information about the external world is exclusively visual the experienced world may be constructed in the same sense as it is by combining the data from other systems. There are many dimensions within vision, dimensions of shape, color, and location and movement in three dimensions, and information about these dimensions may be distributed through much of the brain. In fact, one characteristic of the brain's normal work is the extent to which different regions participate in particular jobs.

The question we ask about the origin of mind is: When in the evolution of the brain did it become necessary to construct a representation of reality rather than work directly, in reflex fashion, with "raw" neural information? While most vertebrates almost certainly are adapted to use a representational method of handling information, with encephalization to an avian or mammalian grade, creating a model of reality would have become essential for coordinating information from the external world in an effective way. Although we need not imagine the origin of mind as exclusively a result of encephalization, it is appropriate to imagine mind as having become a much more complex construction in the mammals. Because of the extraordinarily great amount of neural information that has to be handled, we have to imagine that the processing is hierarchical and that the actual construction of a model of a real world is a function of some level or levels in the hierarchy.

Mind refers to knowledge of reality. I emphasize that this knowledge must be achieved by constructing a model of the real world and that the knowing is of the model rather than direct knowledge of the external world. The real external world is transformed into a model that can be experienced, and knowledge and action are referred to that model. We know that the model can sometimes be false or misleading, as in some illusions and in some familiar perceptual demonstrations. But most of the time the model works well as a framework for behavior. We don't normally know when it fails, because we don't normally know the external world independently of this construction by the brain. When we have independent knowledge, i.e., from the readings of physical instruments or from arranging patterns of stimulation for others to experience (i.e., per-

forming experiments on perception), we can recognize the constructed and sometimes fallible nature of our normal experience. I am arguing that the construction of such a mind was a necessary consequence of the adaptive demands faced by the earliest mammals. The adaptations for integrating information from several sense modalities about the same events at a distance were, in effect, the creation of mind as a knower of reality.

A Hominid Scenario: The Evolution of Language

The evolution of a prehominid anthropoid into a hominid species occurred perhaps 4 or 5 million years ago, and present evidence is that we humans share our prehominid ancestor with living chimpanzees. This provides some clues about our mental origins, since we know a fair amount about the mental capacities of chimpanzees (Kummer and Goodall, 1985; Passingham, 1982; Premack and Woodruff, 1982). We know, for example, that we share with chimpanzees the conservation of mass as discussed by Piaget (Premack and Kennell, 1978); the ability to make, use, and train others to use primitive tools (Boesch and Boesch, 1983); and educability in the use of languagelike symbols (Savage-Rumbaugh et al., 1985). We also share the ability to learn to distinguish ourselves from others on the basis of fairly abstract information, such as that provided by a reflection in a mirror (Gallup, 1979), which indicates that the knowledge of the self as an object is rather well developed.

These shared behavioral traits were presumably in the repertoire of our common ancestor, which means that we evolved from a species that had the mental capacities required by those traits. Some, but not all, of these capacities are shared with the other two great ape genera, the oranges and gorillas, as well as with chimpanzees, but no one has yet demonstrated that other anthropoid primates, that is, monkeys and gibbons, possess them. The evidence is not all in on just how much is shared, nor does everyone agree on how to interpret the behavioral data as evidence of cognitive capacities, but we and the great apes appear to be closer relatives with respect to those capacities than either of us are to other anthropoids.

Among the more spectacular recent discoveries on our shared

capacities has been the educability of chimpanzees and other great apes in the use of "language" initiated under human tutelage as discussed by the Gardners and others (Gardner and Gardner, 1985). I am as impressed as everyone else by the remarkable performance, but I believe that the extraordinary performance of chimpanzees in languagelike activities involves other (impressive) cognitive capacities. My reactionary view (contradicting that of my friends in the ape-language field) is that our use of language is uniquely human, and I hold it on the basis of the logic of an evolutionary analysis and scenario.

My scenario follows the same general form as my analysis of the beginnings of mammalian encephalization. It begins with the neurological status of language, namely that it is controlled by an enormous *neocortical* system. As I emphasized earlier, I interpret neocortical control as implying that at the most fundamental level, the system that is being controlled is perceptual and cognitive. Human language is, therefore, to be considered a priori a perceptual-cognitive adaptation.

In seeking to identify selection pressures that were effective during the prehominid-hominid transition and were met by a languagelike adaptation, I sought to identify problems of adaptation that required unusual perceptual-cognitive capacities. I recognized, of course, that those capacities would not necessarily have resembled language as we know it although they had to evolve into such a language capacity. The role of language in human communication had to be secondary both in time and in importance according to this evolutionary analysis, since pressures for improved communication would have led to a different kind of initial adaptation, which would not have required much expansion of the brain for its control. But even in its beginnings, language may have been preadaptive for present human language and its place in communication, and it was according to my scenario.

The first step in this evolutionary narrative is to suggest for the ancestral species an environmental niche characterized by adaptive requirements that would put unusual demands on the already large perceptual-cognitive brain system of a prehominid or early hominid. The environmental requirements, I propose, were in the climatic

change in the Mediterranean basin, which reduced the size of the normal forest habitat for a chimpanzeelike primate species—the prehominid of my scenario. As I imagine them, some individuals of the prehominid populations were adapted to live in the desertlike or savanna region at the forest's edge and were able to shift to a more carnivorous diet than that typical for primate species (cf., Pilbeam, 1984). It was in the neurogenetics of those individuals that I would identify the precursors of language.

The niche that was available was for a carnivorous predator, but the animals that invaded it successfully were social vocal primates similar to living chimpanzees, and not members of the order Carnivora. The model of a species adapted for such a niche is the well-studied timber wolf (Peters and Mech, 1975), a proper social carnivore, with a proper profile of morphological, neural, and behavioral adaptations for life in this niche. There are information-processing requirements for the adaptations that are fulfilled easily by wolves, which are average mammals in encephalization. But meeting those requirements would strain the neural processing capacity of an anthropoid primate species, despite its being more than twice as encephalized as wolves, because anthropoid primates lost the capacity to use certain critical information during the course of their evolution. My view is that the specialized information processing requirements were met in our hominid ancestors by a new adaptation that eventually evolved into human language.

The special demand of this niche is that it involves the navigation of a very large territory and range by a socially integrated group of predators to harvest prey in sufficient numbers to support the predators. In living wolves a typical territory is of the order of several hundred km². In contrast, a typical daily range of living gorillas and chimpanzees for normal foraging may be only a few hundred square meters (Pickford, 1988). A successful predator must *know* its territory, and this means that it must have a good cognitive map of it and remember the map's history and status. The sensory and neural equipment of wolves, in contrast to that of apes, provides the clue for the new anthropoid adaptation that was required and which appeared in our hominid ancestors.

For their adaptations as social predators, wolves have an elaborate

scent-marking system coupled with “normal” olfactory bulbs (more than 50 times the size of the almost vestigial human olfactory bulbs) and presumably excellent olfactory sensation and perception. The brain systems receiving the olfactory information include the piriform lobes and schizocortex, and certainly hippocampus. We know very little about how olfactory information is used in cognition, since we humans are peculiarly deficient in that sense modality (see fig. 12), and our intuitions about it in “normal” mammals are bound to be inadequate. Olfactory information in living carnivores is known to be sufficient to enable individuals to identify other animals individually (Brown and Macdonald, 1985; Rasa, 1973; Roeder, 1983), and we probably should think of it as having a role comparable to that of vision in our lives. This means that it could be used to create maps formed with edges and borders and so forth, and populated by animals and other objects—at least we should imagine this as something that can be constructed from olfactory data.

The fate of these maps in controlling action would be comparable to that of a well-remembered map in our own lives. Mapping and memory about maps are among the functions that appear to involve important hippocampal control (Horn, 1985; Squire, 1987), and the system for wolves presumably involves significant sensory analysis of scent marks, coupled with the establishment of appropriate cognitive maps, with access to all of the mapping and memory functions in which hippocampal control occurs. We should imagine the real world constructed by a wolf from olfactory information to involve input from olfactory bulbs coupled with appropriate analysis by hippocampus, paleocortical, and neocortical structures to produce a “model of reality” that corresponds more to the one we can build from visual information than to the one we build (or fail to build) from odors.

The neurobiological problem of an anthropoid species adapting to a social predator’s niche is somewhat analogous to that of a visual “reptile” species adapting to a nocturnal (mammalian) niche. An anthropoid primate has the right central neural machinery for the adaptation—appropriately large hippocampus and related structures. But in figure 12 you see the evidence that the system as a whole, which is coupled peripherally to the olfactory bulbs, would

be unlikely to work well with the almost vestigial olfactory bulbs of anthropoids. (The adaptational problem is like that of a species with vestigial eyes and retina, evolving under selection pressures to have access to the central visual system.) A solution to the adaptational problem could take advantage of the fact that the hippocampus, which may be thought of as the neural central processing unit in the brain's control of the required cognitive adaptation, is a polysensory structure that can be accessed by other senses. My idea is that the transition to the hominid grade was correlated with the evolution of other peripheral access to the cognitive system that controls a predator's mapping of its range, and primarily by the use of the auditory-vocal channel, which is highly developed in primates.

It is an odd picture, but I think it works. Instead of urinating and sniffing (the scent-marking and sensing that wolves do), we can imagine our ancestor as marking with sounds and sensing the sounds—talking to itself, as it were, but in primitive tongues. The picture is odd, but no odder than another use of an auditory-vocal channel that evolved in some cetaceans and in insect-eating bats, in which echoes from vocalizations are used in the elaborate sonar system that evolved in these species, and from which they construct and know the external world. The picture for our ancestors would be adequate for access to the cognitive systems for mapping and remembering important features of the external world, that is, for knowing that world. The vocalizations would constitute a very small vocabulary but a vocabulary. A model for that might be the three “word” vocabulary of vervets to signal the presence of eagles, or leopards, or snakes. The hominid vocabulary would have to be larger to encode relevant environmental features, and less frenetic, not a danger signal that commanded escape but a knowledge signal that helped construct a map of the world.

The suggestion is, in summary, that an auditory-vocal system was established for marking and knowing a territory or range, that this system sent information to appropriate old-brain and neocortical systems, and that the information was integrated with other knowledge of the external world. (An important peculiarity of the system, only interjected here but worth much more discussion, would be that even at its “sense-data” stage, this system would be neocorti-

calized, because it would appear in a species in which the sensing and marking “vocabulary” was already neocorticalized.) It was a new perceptual-cognitive system and could interact with the very elaborate older system based on vision and touch and other senses, which was already in place. The latter system is the one that enables living chimpanzees to be so much like humans in so many ways, but it is a system that we probably know in a distorted way. Our own knowledge of the external world is much more elaborate—built not only from that sensory mapping that we probably share with other anthropoids and sometimes philosophize about, but by important inputs to the mapping that comes from our language “sense” as it has evolved in *Homo sapiens*.

This scenario offers a solution to an adaptational problem: how an anthropoid can succeed as a social predatory mammalian species without normal olfactory bulbs. It also has implications for other aspects of hominid evolution, because it describes a new cognitive system that is obviously usable for communication with conspecifics. Communication with the auditory-vocal channel is common in primates, as warning calls and other social messages that elicit a variety of behaviors. The communication by hominids using their range-marking system would be of a new kind, however, because the information transmitted by the auditory-vocal channel would be incorporated directly into the listener’s knowledge of the external world rather than act as a releaser or elicitor of specialized behavior. Let me elaborate on this odd notion.

As I have pointed out before, animal communication is normally a system of commands to other animals that can be thought of as having coevolved with the system of responses to those commands. The vervet calls are good examples of what I mean. We can think of the calls as danger signals that elicit appropriate escape action as the normal response. The cognitive dimension of this interaction could be completely absent; it probably is absent in most danger signals in most species, although for other reasons we can assume that it is present in vervets. In any case, normal animal communication need have no cognitive dimension.

The feature of human language that my scenario would emphasize is that it began as a cognitive rather than communicational adap-

tation. That it evolved into the characteristic communication system of our species implies that our communication is not like that of other mammals. Once the adaptation of using auditory and vocal signs to label the geographic environment had appeared, its utility for communication compared to normal communication with sign stimuli that release "instinctive" behaviors in other members of the species is fairly obvious. This cognitive system for knowing an extended range, when used to communicate with another animal, could communicate the knowledge of the range, or other knowledge. What individual A knew could become part of what individual B knew if B merely listened while A vocalized. The only other species in which something close to this is believed to occur are echo-locating bats, which can intercept one another's calls and their echoes, and, in that sense, experience one another's worlds. I have speculated that this sort of thing could have developed in dolphins as well, and that the additional neural machinery in the dolphin's brain might process such information into something more nearly like human language (Jerison, 1986).

I should state this conclusion about language more dramatically. Since language contributes to our knowledge of reality in the same general way as information received by the conventional senses, such as the eye and ear, when we communicate with language we communicate information that contributes to our reality. The listener or reader receiving the message incorporates it into his or her reality and then *knows* the same world that we know as we communicate. Communication with language is, thus, a sharing of awareness or consciousness. We literally read minds when we read a realistic text and enter the minds of the characters as if we were living their fictional lives. This very common experience is really very odd, and it is one of the stranger features of the human mind.

Consciousness

This view of language leads to an unusual view of the nature of human consciousness in an evolutionary framework. As I mentioned before, there are two aspects of consciousness. The first, and biologically most important, is in connection with one's knowledge of

the external world and should be thought of as the problem of awareness, or representation, or imagery. Why do we know a pictorial world with solid objects and so on? I say that this is the more important biologically, because I believe that the evidence is overwhelming that all birds and mammals are conscious in this sense, and this may also be true for other vertebrates. I mentioned Herrnstein's work with pigeons, which can identify faces that people miss. Griffin (1976) has argued for a universality for this kind of consciousness, or awareness, in an appropriately persuasive way. From my perspective, this means that in most vertebrates, certainly in birds and mammals, the work of the brain includes the construction of a possible real world from sense data, and that "possible world" is the reality that the animal knows. The function of this construction is to make sense of an otherwise overwhelming mass of neural data that refers to the external world.

The other kind of consciousness involves an awareness of self that is unusual. It is not only the self as an object, which is really the same as any other object of which one may be aware or conscious in the first sense. It is the knowledge that the self is different from other objects in that it generates knowledge and knows that it knows. Why would this kind of self be created by a brain? A functional explanation is that this kind of self is necessary if one is to have human language as a dual adaptation for both perceptual/cognitive uses and for communication. Our knowledge of the external world is too important to be compromised by confusion about where it came from. If we can know another's external world simply by hearing (or reading) some statements, it is important that we be able to distinguish this known world from the reality that we know when our information comes through the usual sensory channels, e.g., when we see and hear and touch the external world. We can also know an external world by remembering it, and if our memories are verbalized that information, too, can enter into our awareness of the moment as information about the external world. The point is that language is so potent a medium for knowledge that it may be essential that knowledge carried by that medium be distinguished from other knowledge. By being self-conscious, we can distinguish images generated by the spoken or written word from images gen-

erated at the sensory and motor surfaces of the body in interaction with nonverbal external information. We can distinguish image from reality. It is another oddity about the mind that we don't always succeed in making the distinction, as any schizophrenic and many mystics and dreamers can tell us.

CONCLUSION

Mind is a construction of the brain, and it evolved as the brain became enlarged during the course of evolution. Mind is a necessary brain adaptation that organizes otherwise unmanageable amounts of neural information into a representation of the external world. Many unusual specialized adaptations have appeared in the course of evolution in connection with the evolution of information processing with respect to the external world, and in mammals most of these almost certainly involved aspects of mind, such as awareness of reality. Human language is one such specialized adaptation, and according to my analysis it is the explanation for the unusual human experience of self-consciousness, that is, of the awareness that we are aware and that we are knowers—that we have minds.

ACKNOWLEDGMENT

My lecture as delivered was prepared in the summer of 1989, during my tenure as a visiting professor at the Max-Planck-Institut für Biologische Kybernetik, in Tübingen, and I thank Valentino Braitenberg, director of the Institute, for his hospitality and comradeship. I thank especially Almut Schüz, my collaborator at the Institute, who, among other things, supervised the work that became figures 5, 6, and 7. I also thank the staff at the Institute with whom I worked most closely: Monika Dortenmann, Margarete Ghasrol-dashti, Claudia Martin-Schubert, Uli Wandel, and Shirley Wuerth. Although in a sense everybody listed in my references should be acknowledged, I want to thank a few colleagues in particular. Roland Bauchot ungrudgingly shared his entire collection of as yet unpublished data on fish allometry. Dean Falk, Zofia Kielan-Jaworowska, R. D. Martin, the late Len Radinsky, Sam Ridgway, Wally Welker, and Jack Wilson provided brain and endocast material. I relied

heavily for documentation in this expanded written version of the lecture, on data collected over many years by Heinz Stephan and his colleagues. I also want to thank Paul Harvey, William Hodos, Michel Hofman, and Phillip Tobias, as well as the colleagues mentioned earlier, for many stimulating discussions on various aspects of my topic. Finally, I must thank my wife, Irene, who is my best editor, critic, and friend, for her continuing support.

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*Published versions of these lectures can be obtained from Publications, Dept. of Anthropology, The American Museum of Natural History, Central Park West at 79th St., New York, N.Y. 10024.

**Out of print.

†Published version: *The Brain in Hominid Evolution*, New York: Columbia University Press, 1971.

JAMES ARTHUR
1842-1930

Born in Ireland and brought up in Glasgow, Scotland, James Arthur came to New York in 1871. Trained in mechanics and gear-cutting, he pursued a career in the manufacture and repair of machinery, during the course of which he founded a number of successful businesses and received patents on a variety of mechanical devices. His mechanical interests evolved early into a lifelong passion for horology, the science of measuring time, and he both made some remarkable clocks and assembled an important collection of old and rare timepieces.

Early in this century James Arthur became associated with the American Museum of Natural History, and began to expand his interest in time to evolutionary time, and his interest in mechanisms to that most precise and delicate mechanism of them all, the human brain. The ultimate expression of his fascination with evolution and the brain was James Arthur's bequest to the American Museum permitting the establishment of the James Arthur Lectures on the Evolution of the Human Brain. The first James Arthur Lecture was delivered on March 15, 1932, two years after Mr. Arthur's death, and the series has since continued annually, without interruption.



James Anthony

EVOLUTION OF THE BRAIN AND COGNITION IN HOMINIDS

Comparative genetic analyses indicate that chimpanzees and people are descended from a common ancestor (CA) that lived in Africa approximately 5 million years ago (fig. 1). The CA was probably small, with long arms and large canines like those of living apes. Early on, certain descendants of the CA began walking habitually on two legs. At that point, these individuals ceased to be apelike protohominids and became the first true hominids, known today as australopithecines. As can be seen in figure 1, by 2 million years ago, australopithecines had given rise to the genus *Homo*, which eventually led to modern people.

In the late 1970s, a remarkable discovery of fossilized hominid footprints occurred at a site known as Laetoli, in Tanzania, East Africa (Leakey and Hay, 1979). Ironically, these 3.5 million year old footprints profoundly changed the then accepted view that hominid brain evolution was intimately linked to the evolution of bipedalism and its consequent freeing of forelimbs, production of tools, etc. Although the makers of the Laetoli footprints were bipedal, brain size in australopithecines that lived over 3 million years ago was in the apelike range, i.e., around 400 cm³ (Falk, 1987b). Indeed brain size, which remained conservative throughout australopithecine evolution, did not begin to increase dramatically until well over a million years *after* the Laetoli hominids took their walk, and then it did so only in the genus *Homo* (fig. 2). Thus the origin and initial evolution of bipedalism *preceded* the dramatic increase in brain size that characterized *Homo*.

Three and a half million years after the Laetoli footprints were made, another famous set of footprints appeared—this time left on the moon by the astronaut Neil Armstrong (Falk, 1991). The feet that made the impressions at Laetoli and those that left footprints on the moon were, for all practical purposes, the same (Tuttle, 1985). The part of the anatomy that differed between the earlier Laetoli hominids and the later astronaut was not the feet but the brain. What happened to the brain during hominid evolution that permitted Armstrong's species to place him on the moon? Referring to

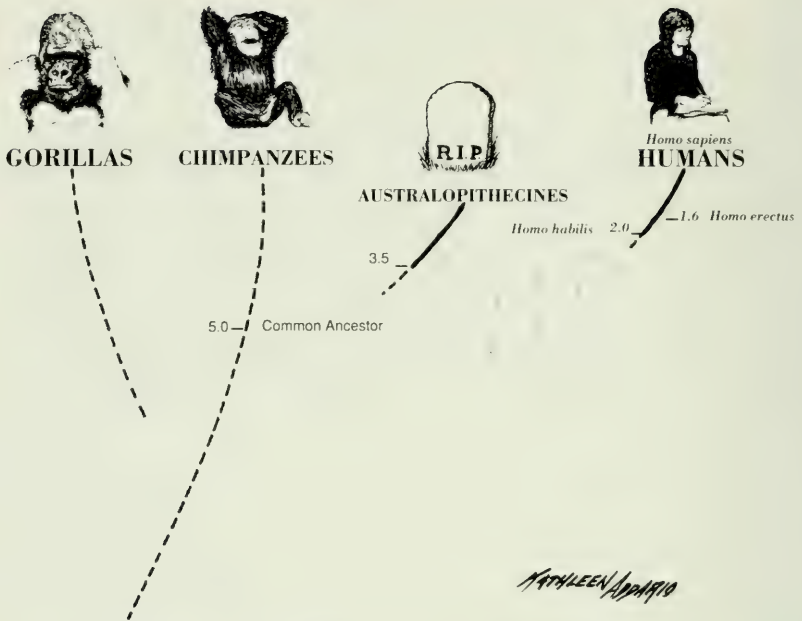


Fig. 1. Molecular evidence suggests that people and chimpanzees are descended from a common ancestor that lived approximately 5 million years ago. The fossil record for australopithecines and for *Homo* is indicated by solid lines. (Reprinted from Falk, 1991)

figure 2, this question may be divided into three parts: (1) What modifications occurred in the direct ancestors of *Homo* that facilitated or permitted the initial take-off in brain size? (2) Once brain size began to increase, how was the continued increase in brain size sustained, i.e., what behavior(s) were “targeted” by natural selection? (3) How did the external and internal organization of the human brain change as it enlarged and what were the cognitive correlates of these neurological changes?

Paleoanthropologists use two methods to address these questions. The “direct method” relies on examination of fossil hominids for information about the external morphology of the convolutions and blood vessels of the brain (as reflected on casts of the interior of the braincase, or endocranial casts), and for estimates of brain size (which is approximated by cranial capacity). These features may then be interpreted in light of information determined from other parts of

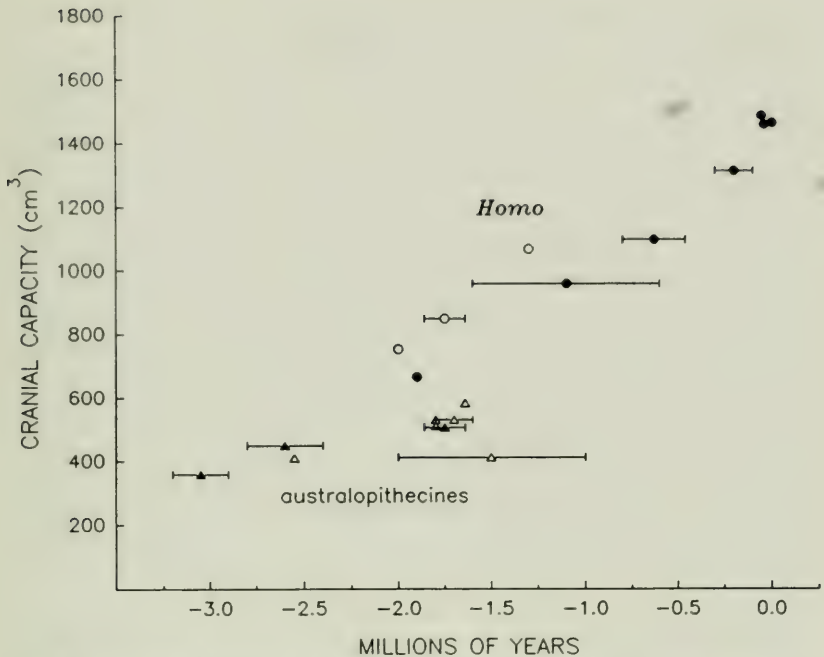


Fig. 2. Cranial capacities of hominids plotted against time. Triangles represent australopithecines, circles *Homo*. Filled symbols indicate more than one individual in the sample. Cranial capacity increased markedly in *Homo* but not in australopithecines. (Reprinted from Falk, 1991)

the skeleton (e.g., body size, dietary preferences), as well as the archaeological record that pertains to culture, climate, and habitat. The “comparative method,” on the other hand, is based on studies of the brains and cognition in monkeys, apes, and humans, along with the assumption that these primates approximate an evolutionary sequence. Because they share a fairly recent CA with humans, chimpanzees are especially important in comparative studies. Although the fossil record provides broad outlines that may be used to describe hominid brain evolution, the finer details must be filled in by synthesizing information from comparative psychology and comparative neuroanatomy/neurophysiology. Using these methods, each of the three questions outlined above will be discussed in this lecture (with particular attention to the third).

I. WHAT FACILITATED THE INITIAL TAKE-OFF IN BRAIN SIZE?

Discovery of the Laetoli footprints has caused paleoanthropologists to abandon the belief that bipedalism was intimately linked to an increase in brain size in early hominids. The feet went first. But why? As is frequently the case in evolutionary studies, a clue to this mystery may be found by examining the environment of the particular group of australopithecines that gave rise to *Homo*. These early hominids (known as gracile australopithecines) are believed to have spent their days roaming across open savanna grasslands in search of widely dispersed food, water, and trees. A number of workers have speculated that australopithecines were probably subject to intense solar radiation as they went about their business in the tropical savanna habitat (Wheeler, 1988). This is significant for hominid brain evolution because brains are exquisitely heat sensitive. In fact, according to one noted vascular physiologist:

A rise of only four or five degrees C above normal begins to disturb brain functions. For example, high fevers in children are sometimes accompanied by convulsions; these are manifestations of the abnormal functioning of the nerve cells of the overheated brain. Indeed, *it may be that the temperature of the brain is the single most important factor limiting the survival of man and other animals in hot environments* (Baker, 1979: 136, emphasis added).

For various reasons, I have hypothesized that selection for specific vascular features that controlled brain temperature released a physiological constraint on brain size, which then became a focus of natural selection in *Homo* (Falk, 1990).

The Radiator Theory

If a species evolves a new form of locomotion or habitual body posture, its circulatory system will be modified because of changed gravitational (or hydrostatic) forces associated with the new mode of life. Hydrostatic pressures may be envisioned by imagining a long tube half-filled with water. If the tube is horizontal, the water (and associated gravitational stress) is distributed along its entire length. However, if the tube is tilted to the vertical, all of the water is in its bottom half and that part of the vessel takes the stress from the

weight of the fluid. Natural selection favors vascular systems that are designed to cope with hydrostatic stresses. For example, arboreal snakes have evolved special mechanisms for pumping blood through vertically oriented vessels, as opposed to the situation in their horizontally inclined relatives (Lillywhite, 1987a, 1987b).

For physiological reasons, the circulatory systems of early hominids *had* to become modified during the evolution of bipedalism. Indeed, evidence of those modifications appears in modern humans. Because people sleep horizontally but move about in the world vertically, they have complex vascular systems that are designed to cope with hydrostatic pressures in a variety of postures by shifting the flow of blood with changing body position. Thus, if a person is lying down, blood flows out of the skull through the internal jugular veins. When the individual stands up, however, most of the exiting cranial blood shifts away from the jugulars and into a network of veins that surrounds the spinal cord. (Monkeys and apes have vascular systems that are tailored somewhat differently to their own forms of locomotion.)

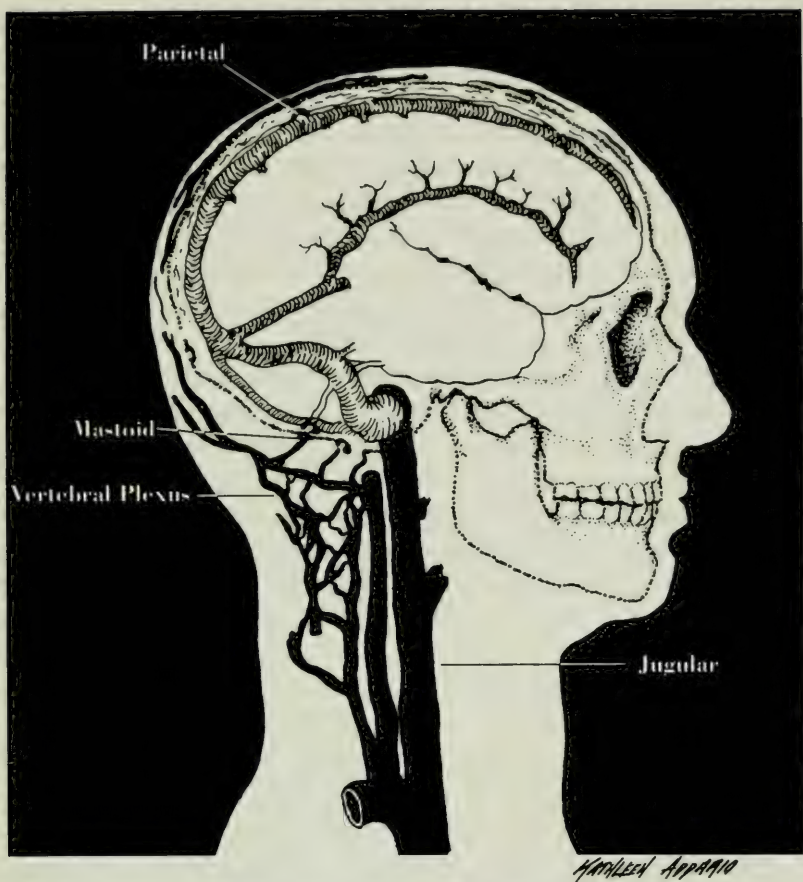
Fortunately for paleoanthropology, certain details of the cranial vascular system appear in skulls of fossil hominids. These features include grooves that represent venous sinuses and meningeal vessels, as well as emissary foramina through which emissary veins penetrate the skull. Taken together, these features show that the cranial vascular systems of different groups of early hominids were adapted in one of two different ways as each group refined bipedalism in its own particular environment. On the one hand, the hominids from Ethiopia that are associated with the famous “Lucy” skeleton have an unusual venous sinus in the occipital region (the “occipital/marginal” sinus) that they share with later living australopithecines who were probably their descendants (Falk and Conroy, 1983). These australopithecines (known as robust australopithecines) ultimately became extinct without giving rise to more modern hominids. On the other hand, data regarding the emissary veins suggest that a different cranial vascular system developed in the gracile australopithecines who lived in thermally stressful habitats and eventually gave rise to *Homo*.

Innumerable tiny veins penetrate the outside of the human skull

and communicate with the diploic veins that are found within the bones of the skull itself. The diploic veins, in turn, penetrate the inside surface of the skull bones, where they communicate with meningeal veins that course on the surface of the dura mater that covers the brain. Thus, the human skull is covered on its outside and inside surfaces with a complex web of communicating veins that happen to lack valves. Significantly, several named emissary veins that are part of this network penetrate through specific foramina of the skull. Consequently, the presence of emissary veins can be surmised from fossil crania. Comparative data from skulls of living apes and humans (Boyd, 1930) and direct data determined from the hominid fossil record (Falk, 1986) reveal that frequencies of the mastoid and parietal emissary foramina increased dramatically in the lineage leading from gracile australopithecines to extant *Homo*, but not in the other early hominids (fig. 3). Moreover, the frequencies of these emissary veins seem to have increased in step with increasing cranial capacity (Falk, 1990). If emissary veins are viewed as a "window" into the wider network of cranial veins, these data suggest that cranial vasculature became increasingly complex as evolution progressed and brain size increased in *Homo*. What function could this network of veins have served?

The answer to this question is provided by physiological research that compared the direction of blood flow in emissary veins of human volunteers who were subjected to severe cold stress at one time, and heat stress at another (Cabanac and Brinnel, 1985). Cabanac and Brinnel found that under conditions of hyperthermia, cranial blood that had been cooled by the actions of sweating and evaporation at the scalp was brought from the outside surface of the skull *into* the brain case. (In cold subjects, on the other hand, blood flow was slow and flowed out from the cranium.) The researchers concluded that the entire network of cranial veins which the emissary veins represent functions to selectively cool the brain under conditions of severe heat stress. Thus, like the engine of a car, the human brain has a radiator that prevents overheating.

To summarize the radiator theory, evolution of a prototype network of cranial veins in gracile australopithecines released a thermal constraint that had previously kept brain size in check. This facil-



MARILEEN APPARAO

Fig. 3. The mastoid and parietal emissary foramina and the vertebral plexus of veins that receives cranial blood when people are upright. The emissary veins are part of a wider network of cranial veins that communicate between the outside and inside of the skull. This network helps cool the brain under conditions of hyperthermia, and also drains blood to the vertebral plexus. (Reprinted from Falk, 1992)

itated the take-off in brain size in *Homo*. Bipedalism in gracile australopithecines preceded the increase in brain size in *Homo* for two reasons. First, because of the constraints of gravity, bipedalism necessitated a rearrangement in cranial blood vessels. (Since this was also true for robust australopithecines, it was a necessary but not sufficient condition for the subsequent evolution in brain size.) Second, bipedalism allowed gracile australopithecines to minimize the

amount of body surface exposed to the sun, thereby reducing their heat loads and making it easier to adapt to thermally stressful savanna habitats (Wheeler, 1988). Thus, the vasculature of gracile australopithecines became modified in response to gravitational *and* thermal pressures that were associated with refinement of bipedalism on the savanna. One result was the beginning of a cranial radiator network of veins that could help cool the brain under conditions of intense exercise. More important, once in place, this system was itself modifiable and could therefore keep up with the increasing thermolytic needs of an enlarging brain.

The radiator theory is mechanistic. The dramatic increase in brain size in *Homo* is viewed as having simply been *facilitated* by the release of thermal constraints that previously kept brain size in check. Thus, the radiator network of veins is seen as a prime releaser, not a prime mover of brain evolution. One must turn to other theories for speculation about the behaviors that were selected for once the brain had acquired an adjustable radiator and *could* get bigger.

II. WHAT BEHAVIORS WERE TARGETED BY NATURAL SELECTION?

Brain size doubled during the past 2 million years in the genus *Homo*, increasing from an average of approximately 700 cm³ to a modern mean of about 1400 cm³ (fig. 2). Although body size (or stature) also enlarged during this time, it did not keep up with the increase in brain size. Consequently, the brain of humans is three times as large as is mathematically expected for an ape of equivalent body size (Passingham, 1975; Falk, 1980b). What factors were responsible for the sustained increase in brain size? Since at least Darwin's time, scientists have attempted to answer this question by identifying specific behaviors that were the primary target of natural selection. Some workers have gone so far as to suggest that a single behavior was responsible for human brain evolution. Classic "prime mover" candidates include warfare, language, tool production, and hunting. These are discussed elsewhere (Falk, 1980b). Two new candidates may now be added to this list—throwing (Calvin, 1982) and social (or Machiavellian) intelligence (Byrne and Whiten, 1987).

According to Calvin's (1982) throwing hypothesis, one of the earliest lateralizations that occurred in the hominid brain was for rapid motor sequencing of the right hand and arm (represented in the left frontal lobe). Calvin believes that the cause of this lateralization was natural selection for right-handed throwing of stones at prey. He further suggests that neural machinery for throwing may also have been used for the oral-facial musculature (which is represented near the hand in the brain) and that, if so, this sequencing machinery provided the scaffolding for the subsequent development of another left hemisphere product, human language. Although the throwing hypothesis is consistent with some research concerning neurophysiology of the motor cortex (Ojemann, 1983), the assertion that skilled throwing *preceded* the evolution of language remains interesting but speculative.

Because nonhuman primates are extremely complex in their social relationships, primatologists have recently focused attention on social intelligence as a possible prime mover of brain evolution. For example, Byrne and Whiten (1987) hypothesize that selection occurred for "Machiavellian intelligence" in which individuals relentlessly selected for still more cleverness (including deceptive behavior) in their companions. Other workers extend this concept by suggesting that humans evolved as a result of a process of "runaway social competition" between competing groups (Alexander, 1989). This latter form of "intelligence" shades into another prime mover candidate, namely warfare. A problem with social intelligence as a prime mover of hominid brain evolution is the fact that many species of nonhuman primates are extremely clever in their social interactions, yet without benefit of the extremely encephalized brain that characterizes humans.

As discussed elsewhere (Falk, 1980b), although entertaining, the search for prime movers of human brain evolution is highly speculative and does not lend itself well to hypothesis testing. Furthermore, whether or not it is reasonable to attribute all of hominid brain evolution to selection for only one behavior is debatable. As described below, the human brain underwent a remarkable reorganization as it enlarged. One would suppose that if selection of one behavior was primarily responsible for brain evolution in *Homo*,

that behavior would be tied functionally to the neurological reorganization that occurred. It should also clearly distinguish all people from other primates. These issues will be returned to later.

III. NEUROLOGICAL REORGANIZATION AND ITS COGNITIVE CORRELATES

Under some circumstances, details of the cerebral cortex, blood vessels, venous sinuses, and sutures are reproduced on casts of the interior of the braincase (endocranial casts or endocasts). Endocasts may occur naturally when fine sediment consolidates inside a skull or can be prepared artificially with latex. One limitation of endocasts is that the relatively largest-brained species within various groups of mammals, including primates, fail to reproduce clear details of the pattern of convolutions on endocasts (Radinsky, 1972). Thus, endocasts from skulls of *Homo sapiens* reveal little information about the surface of the brain, whereas small-brained australopithecines are associated with a fossil record of nicely detailed natural endocasts.

A second limitation of endocasts is that they fail to reproduce all areas of the cerebral cortex equally well. For example, early hominid endocasts usually do not reveal many details from the occipital region of the brain, while the frontal lobe is reproduced in much better detail. Interpretation of the external morphology of australopithecine occipital cortices has been subject to a good deal of controversy, partly because of this limitation. Ralph Holloway believes that the outside surface of australopithecine occipital lobes appears humanlike in certain respects, whereas my comparison of chimpanzee, gorilla, and human brains led me to conclude that australopithecine sulcal patterns are apelike in the occipital and all other regions of the brain (Falk, 1980a; Radinsky, 1979). During the past decade, a good deal has been published on this controversy, and details are available elsewhere (Falk, 1992).

One is on firmer ground with the frontal lobe, not only because it happens to show up better on endocasts, but because it is the one area of the brain in which sulcal patterns clearly distinguish human brains from ape brains (Connolly, 1950). In the frontal lobes of great

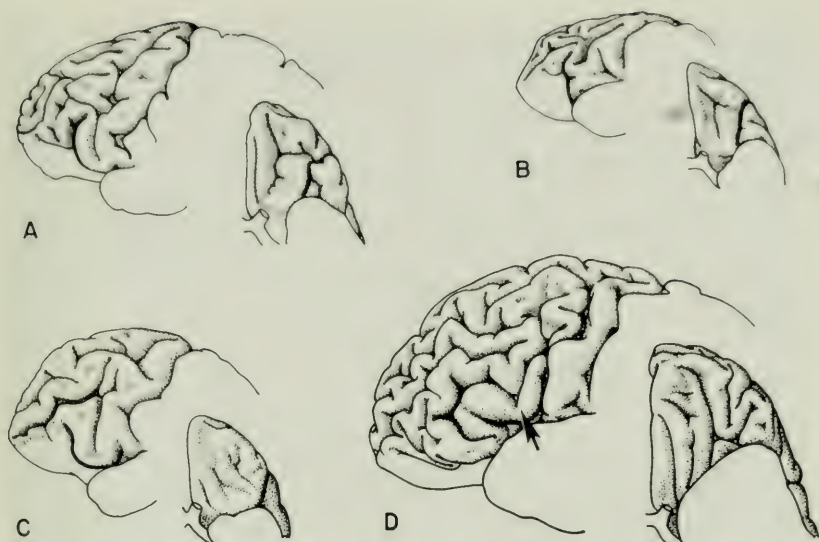


Fig. 4. Left frontal lobes (lateral view above, rotated to basal view below): (A) chimpanzee, (B) orangutan, (C) gorilla, and (D) human. Orbitofrontal sulci are darkened in the ape brains. Sulci darkened in the human brain include the inferior frontal and those limiting the pars triangularis (arrow) associated with Broca's speech area. (Reprinted from Falk, 1983)

apes (fig. 4A–C), an orbitofrontal sulcus (darkened in the illustration) incises the lateral border and continues to course back toward the temporal lobes on the underneath surface. This sulcus is not visible on human brains, however, because it has been displaced deep within the Sylvian fissure by the expanded convolutions of the frontal lobe. Instead, human frontal lobes are usually characterized by two small sulci that delimit a triangular patch of gray matter (arrow in fig. 4D) that forms part of Broca's speech area in the left hemisphere. (As discussed below, although this pattern is generally similar on the right and left sides, the functions of the two hemispheres differ—i.e., the human brain is lateralized.) In keeping with its expanded size and reorganized sulcal pattern, the human brain also has frontal lobes that appear squared in front (from a dorsal view) as compared to ape brains (Falk, 1983).

The earliest indication of a humanlike frontal lobe in the known hominid fossil record occurs in KNM ER 1470, a *Homo habilis*



Fig. 5. Endocranial surface of left frontal lobe of KNM ER 1470, a *Homo habilis* specimen that is a little less than 2 million years old. Dots are reconstructed portion of frontal lobe. hatching represents damaged area. fi, inferior frontal sulcus; arrows indicate sulci that may delimit an area that is homologous with the pars triangularis of human brains. (Reprinted from Falk, 1983)

specimen from Kenya that is almost 2 million years old (fig. 5). Although brain size in this specimen was only about 750 cm^3 (Holloway, 1978), its endocranial surface reproduces the sulcal pattern in the left frontal lobe that is associated with Broca's speech area in living people. This suggests that *Homo habilis* may have been capable of rudimentary speech (Tobias, 1981; Falk, 1983). Corroborative evidence that the frontal lobe was already lateralized in early *Homo* has been provided by an archaeological analysis of stone flakes, which indicates that knappers may already have been right-handed by 2 million years ago (Toth, 1985). (Recall that the speech organs and the right hand are represented by adjacent areas in the left frontal lobe.)

As noted above, the australopithecine endocranial surfaces appear apelike in the sulcal patterns of their frontal lobes. They also lack the squared shape of the frontal lobe that can be seen in the earliest representatives of *Homo*, including ER 1470. Furthermore, these differences between australopithecines and *Homo* are not merely due to scaling (allometric) factors whereby enlarged brains have more sulci than smaller brains. (For discussion of allometry, see Jerison, 1991.) In



Fig. 6. Right hemispheres of a juvenile chimpanzee brain (top), the Taung endocast (left), and a human newborn (right). In all major respects, the Taung endocast appears apelike, not humanlike. (Reprinted from Falk et al., 1989)

order to control for allometry, sulci from the frontal and temporal lobes of the right hemisphere of the Taung australopithecine endocast were precisely measured and compared to corresponding sulci in the brains of a juvenile chimpanzee and a human newborn whose cranial capacity was close to the size of Taung's (Falk et al., 1989). (See fig. 6.) Once size differences had been taken into account, the ratio of the summed frontal lobe sulci of Taung relative to that for the human baby brain was markedly impoverished—even compared to the chimpanzee brain! Since this was not the case for the temporal lobe, it appears that *frontal lobe expansion was particularly dramatic during the subsequent evolution of Homo*.

Other evidence points to the frontal lobes (or the behaviors that depend upon them) as a particular focus for natural selection during the evolution of *Homo*. Using a new gyrification index (GI) that measures the degree of convolutedness in any given location of the brain, Armstrong and her colleagues compared the extent of folding in the various lobes of monkeys, apes, and humans (Armstrong et

al., 1991). They found that whereas the GIs of apes and humans completely overlap in the occipital region, the human brain is much more convoluted in the frontal lobes than are ape brains. The findings for the occipital region suggest that changes in sulcal pattern occurred only when brain size increased and that the occipital cortex in the Taung endocast was therefore probably apelike. Having studied the entire surface of the brain, the authors concluded (on p. 347): "that the proximal cause or mechanisms by which the hominid brain increased in size are more likely to have been either a response to changes in the frontal lobes or to events that influenced all regions of the brain."

Besides language (which will be discussed below), what behaviors were elaborated with the continued expansion of the frontal lobes during the evolution of *Homo*? Although any answer to this question will necessarily be speculative, it is informative to consider frontal lobe functions that occur in monkeys (and presumably apes) and note their elaborations in humans. Because medical research has focused extensively on macaques, the circuitry in the prefrontal cortex and its regulation of behavior are fairly well understood for these monkeys. A major function of macaque prefrontal cortex is to assess memories (symbolic representations related to visuospatial information, emotions, etc.), keep them "on line," and use them to guide motor behavior in the absence of external stimuli (Goldman-Rakic, 1987). According to Goldman-Rakic (p. 406), "many integrated higher-order functions including language, concept formation, and planning for the future may be built on this functional element." In keeping with this, it is well known (from the old days of lobotomies) that damage to the human prefrontal cortex frequently causes disturbances of attention, an inability to use past experience to grasp the essence of a situation, and a loss of the ability to plan ahead. A "flattening" of personality and inappropriate social behaviors may also result from prefrontal damage.

The archaeological record provides glimpses that suggest frontal lobe abilities may have increased along with increasing brain size in the genus *Homo* (at least up to the relatively recent time of Neanderthals). Preparation of even simple stone tools (associated with early *Homo*) takes some ability to keep a task in mind and execute

a plan. Apparently, abilities pertaining to the manufacture of stone tools continued to evolve so that, by 300,000 years ago, *Homo erectus* was demonstrating relatively sophisticated notions of perspective, control of spatial quantity, and an understanding of composition (Wynn, 1989). Although the human propensity for worrying about the future is difficult to gauge from the archaeological record, most anthropologists would probably agree that the first deliberate burials (attributed to Neanderthals) indicate an upper boundary for the appearance of an acute consciousness of time.

Brain Lateralization

Turning our attention to brain lateralization, its evolution may be investigated by comparing shapes of lobes (petalia patterns) in the brains of nonhuman primates and people. Analyses of CAT scans and radiographs reveal that right-handed people tend to have right frontal lobes that project farther and are wider than the left frontal lobes (i.e., a right frontal petalia), whereas their left occipital lobes are usually wider and protrude more (LeMay, 1976; Galaburda et al., 1978). (The reverse condition of left frontal and right occipital petalias is more likely to be found in left-handers.) Petalias give both the brain and the overlying skull a characteristic lopsided appearance that can be detected on endocasts. These shape asymmetries occur in monkeys and apes, but not to the extent that they do in humans (LeMay et al., 1982). The human pattern of left-occipital-right-frontal petalias appears early in *Homo* and, in keeping with the comparative findings, may have been foreshadowed in australopithecines (Holloway and de Lacoste-Lareymondie, 1982).

Not too long ago, it was thought that humans were unique among primates in manifesting asymmetries in lengths and configurations of certain cortical features, e.g., having a longer left Sylvian fissure and larger left planum temporale. Largely because of recent advances in medical imaging, the alternative idea that cortical asymmetries of humans are end products of a long evolutionary history is now supported by comparative evidence regarding sulcal lengths and areas of cortex delimited by sulci. Thus, rhesus monkeys exhibit numerous asymmetries in their frontal lobes including right frontal

petalias (Falk et al., 1990). These asymmetries, which may involve short-term memory for visual information, correlate with functional lateralization for certain vocal and visual processing in macaques. Analysis of a large sample of macaque endocasts revealed that both gross and detailed morphology of the brain are heritable (Cheverud et al., 1990), a finding that is consistent with a hypothetical genetic component for cortical lateralization.

A greater number of cortical asymmetries have been discovered in humans (Falk et al., 1991) than in monkeys or apes, not just in frontal lobes, but throughout the brain. Taken together, the evidence from endocasts of fossil hominids and the comparative data regarding the external morphology of the cerebral cortex suggest that *brain lateralization became more elaborate as brain size increased in Homo*. What were the cognitive correlates of an increasingly lateralized brain during the evolution of *Homo*? One way to approach this question, is first to observe the functional aspects of brain lateralization in people, and then to compare the cognitive abilities of humans with those of their closest nonhuman cousin, the chimpanzee.

The literature on functional brain lateralization in humans is multifaceted and sometimes difficult to interpret because differences between hemispheres are often subtle but statistically significant (Falk, 1987a, 1992). Upon close inspection, however, contradictory data obtained by separate studies may frequently be attributed to slightly different methodologies or to differences in the populations that were tested. For example, the musically sophisticated and left-handers do not test like the general population on certain measures of brain lateralization. Nevertheless, as a result of various kinds of tests (e.g., dichotic listening, tachistoscopic viewing, etc.) performed on enormous numbers of normal and clinical populations, certain generalizations may be made about the specializations of right and left hemispheres (fig. 7).

As illustrated in figure 7, the left hemisphere is associated with language functions, skilled movements (e.g., like those engaged in by over 90% of right hands), and analytical, time-sequencing processes. This hemisphere is also involved in processing positive emotions. The right hemisphere, on the other hand, engages in holistic,

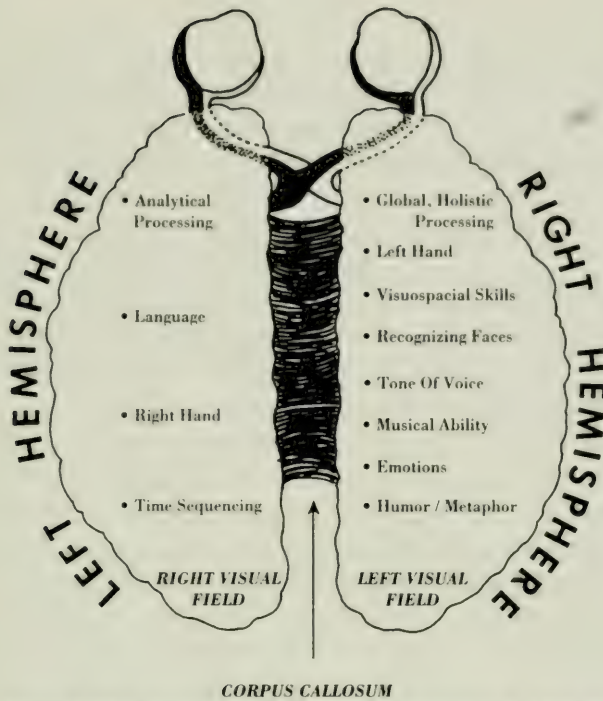


Fig. 7. General specializations of left and right hemispheres. Dorsal view of the brain, which is shown connected by the corpus callosum. (Reprinted from Falk, 1992)

global pursuits. Mental imaging, visuospatial skills, and musical abilities are also associated with the right hemisphere. The right hemisphere processes negative emotions and has a noticeably greater role than the left hemisphere in generally expressing emotions, as well as reading them in other people. In fact, although the left hemisphere processes language, it is the right hemisphere that provides tone of voice, an important and sometimes decisive aspect of verbal communication. The right hemisphere also seems to have an edge over the left in recognizing faces, in the ability to understand metaphor, and in certain aspects of humor. It is important to note, however, that the right and left hemispheres are, of course, connected in normal individuals. (Figure 7 is therefore an oversimplification, i.e., most tasks will have some input from both sides of the brain.)

There is an incredible amount of variation and complexity in the

patterns of asymmetries for various skills expressed by different individuals. Furthermore, males and females seem to be organized somewhat differently with respect to both functional and anatomical brain lateralization. Lateralized behaviors in humans have been hypothesized to be the result of asymmetrical distributions of neurochemicals, as has been shown for certain rodents and birds. Interestingly, it has also been suggested that different patterns of brain lateralization in humans may be the result of developmental events (such as prenatal exposure to testosterone) that differentially influence males and females (Geschwind and Galaburda, 1987). (For further discussion see Falk, 1992.)

One way to assess which behaviors “drove” hominid brain evolution is to compare the frontal lobe and asymmetrically mediated behaviors in chimpanzees and humans (including where the two categories overlap). What do the human and chimpanzee have in common? Beginning with the frontal lobe, both species can bring visuospatial memories on line and carry out related tasks. In fact, chimpanzees are every bit as good as humans at remembering the location of cached food and retrieving it at some later time. Unlike most animals, chimpanzees and humans both recognize themselves in mirrors, a feat that my colleague Gordon Gallup attributes to a frontal-lobe sense of “me” (Maser and Gallup, 1990). Furthermore, both species have fairly good motor skills, e.g., they can work puzzles that require manipulation of parts, and each expresses emotions through gestures that are controlled by frontal lobe motor cortex.

But the similarities stop here. According to Savage-Rumbaugh (Falk, 1992), chimpanzees cannot keep very many tasks in mind at once, the way that humans can. In terms of frontal lobe planning, chimpanzees do not have a humanlike awareness of death or a religion (Maser and Gallup, 1990). With respect to regulating behavior through accessing symbolic representations, chimpanzees are not very good at controlling emotional outbursts—a frontal lobe mediated activity in which almost all human children eventually become proficient. Although they can manipulate objects, chimpanzees as a population are not lateralized for handedness, unlike humans. Finally, the most dramatic (lateralized) frontal lobe differ-

ence between chimpanzees and humans is, of course, that chimpanzees lack the human capacity for speech.

There are other important cognitive attributes of humans (compared to chimpanzees) that depend on an overall lateralized brain (fig. 7). As noted elsewhere:

No chimpanzee ever wrote a book, composed a symphony, painted a realistic portrait, performed a *Singing in the Rain*-quality tap dance, calculated the day of the week upon which a certain date will fall next year, developed a math proof, took apart and reassembled a watch, programmed a computer, designed a bridge, or theorized about the origin of the universe (Falk, 1992: 58).

In short, these human arts and sciences spring from an enlarged lateralized brain that has numerous circuits subserving specialized functions. These circuits are sometimes referred to as modules (Fodor, 1983).

Can these modules be understood in terms of the specific *internal* reorganization that took place in the brain during the course of brain evolution in *Homo*? Since one cannot turn to endocasts for the answer to this question, investigation of brain growth during human development may be informative. Although humans are born with their full complement of neurons, profound changes occur in the nervous system postnatally (Gibson, 1991; Konner, 1991). As the human brain enlarges after birth, there is a proliferation of synapse formation, dendritic branching, and division of glial support cells that form the myelin sheaths around axons (thus giving the white matter its characteristic appearance). Myelination, which increases the speed and specificity of nerve transmission, occurs in specific sequences that appear to correlate with the development of motor, social, and intellectual skills (Gibson, 1991). For example, the appearance of social smiling and fear of strangers in infants is correlated with myelination of specific neurological structures during the first year of life, whereas cortical association areas subserving "higher" intellectual functions continue to myelinate up to the age of 30 years (Konner, 1991).

Comparative studies provide another important source of information regarding hominid brain evolution. Since larger mammalian brains have larger, more widely spaced neurons than do smaller

brains, this trend and other related scaling (allometric) factors probably occurred during brain enlargement in *Homo*. Thus, although the absolute number of neurons would have increased with brain size, their density would have decreased. There also should have been an increase in the overall fraction of the cortex devoted to axonal interconnections (i.e., cortical white matter), along with an increase in dendritic branching. Significantly (see below), the fraction of cells with which any one cell communicates directly ("percent connectedness") would have decreased as brain size increased in *Homo* (Ringo, 1991).

Based on these comparative data, Ringo (1991) has developed an eloquent model that accounts for a general trend toward cortical specialization within larger-brained mammals. As brain size (and therefore neuron number) increases in the various species, each neuron must be connected to a decreased *fraction* of the total number of neurons. Otherwise large brains would be "swamped" by geometrically increasing numbers of connections relative to their absolute number of neurons. (To use Ringo's example, a 100% connected two-neuron system would have two connections whereas a 100% connected four-neuron system would have 12 connections, etc.) Because absolute connectivity nevertheless increases with enlarged brain size, the "interconnection problem" is resolved by decreased neuronal density, i.e., more volume is available per neuron in larger brains. Since long axons take more space than short axons in such a system, they are minimized, and specializations result. In Ringo's words:

One interesting possibility is that this increasing load from interconnectedness is avoided by utilizing specialization so that only within major groupings of neurons need there be full interconnection, while between major groupings only 'results' need to be passed. This then suggests the argument that big brains need hemispheric specialization, because of interconnections getting out of hand, and further suggests that large hemispheres will be more specialized than small ones. This simply means that cortical areas will be more specialized. This tendency appears to follow across the best investigated species. . . . (Ringo, 1991: 5)

Comparative data from prosimians (*Galago*) and monkeys (*Macaca*) suggest that; in keeping with Ringo's hypothesis, new areas were added to the cerebral cortex as brain size increased early in anthro-

poid evolution (Preuss and Goldman-Rakic, 1991). Interestingly, the addition of new areas occurred specifically in prefrontal cortex.

LANGUAGE: THE PRIME MOVER?

What behaviors were targeted by natural selection during the extraordinary neurological evolution of *Homo*? Converging evidence suggests that, during the past 2 million years, changes were especially dramatic in the prefrontal cortex and that, at the same time, overall brain lateralization increased. The prime mover candidate that clearly spans both of these themes is language, which is also the one candidate that clearly separates *all* people from apes. Ringo's (1991) hypothesis, on the other hand, suggests that various concomitant specializations (modules) that are associated with lateralized brains may have been the focus of natural selection. Ringo, however, notes that his theory is general and that it does not preclude specific adaptations for individual species. Thus, any one of numerous specializations that occurred in the enlarging hemispheres could have been selected for during the course of hominid evolution. If selection were strong enough, the end result would have been to fix the target cortical specialization (and its related behaviors) in all members of the population, while retaining a variety of other specializations that are distributed across the cerebral cortex and manifested in varying degrees in different individuals. Since all people talk (but not everyone is musical or mechanically inclined), the frontal lobe's role in accessing symbolic representations, holding them on line, and using them to guide motor output in the absence of external stimuli may have been elaborated during hominid evolution by selection for language-related behaviors. Indeed, the notion of language as a focus for natural selection together with the mechanism outlined by Ringo forms a compelling model that is consistent with much of the evidence outlined in this lecture.

ACKNOWLEDGMENTS

Preparations of this manuscript was supported by NSF grant BNS-9008179. I am grateful to Patrick Ganon, Ken Kramer, Jim Neely,

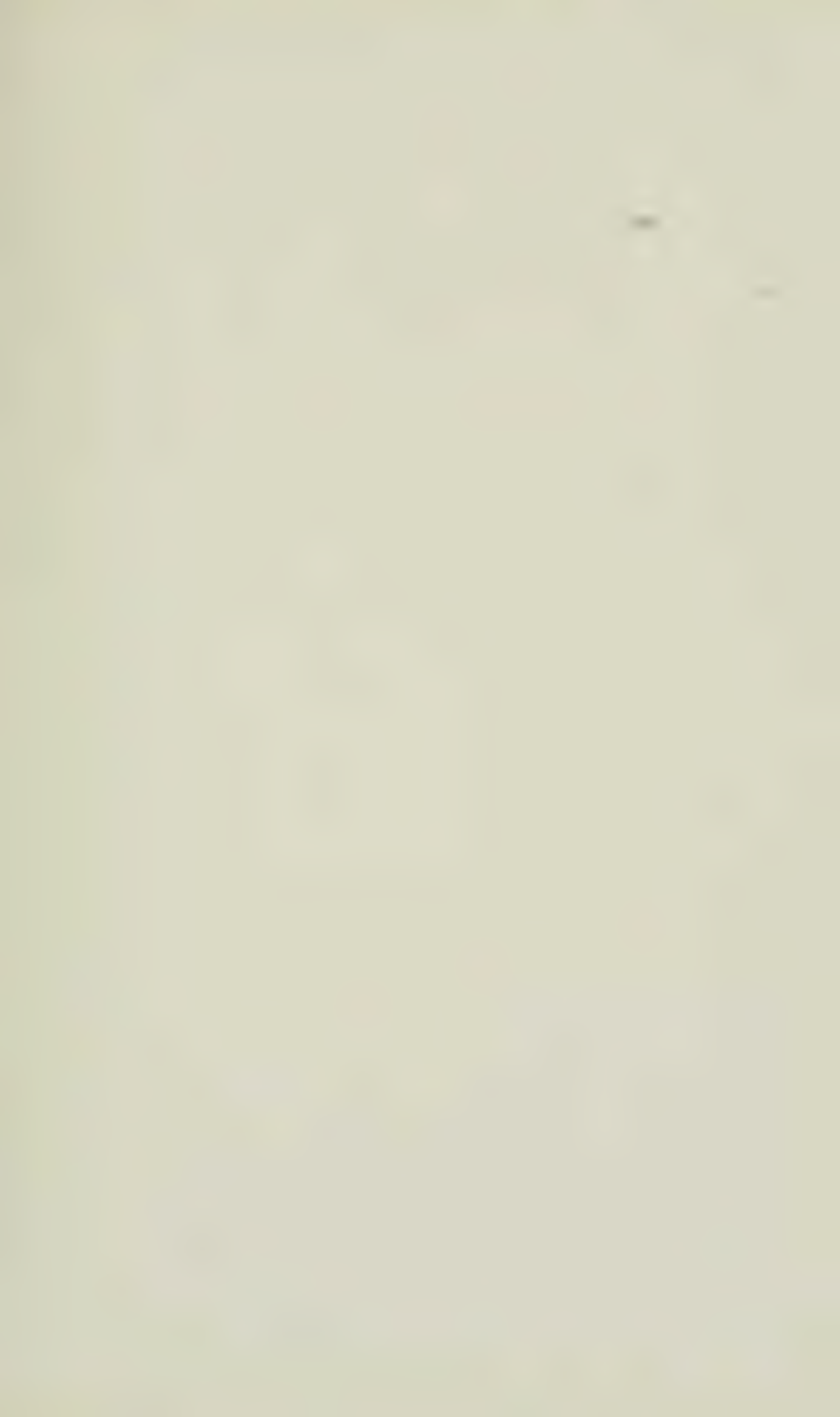
and Ken Weiss for helpful discussions, and to George Gumerman for calling my attention to Neil Armstrong's moonprints.

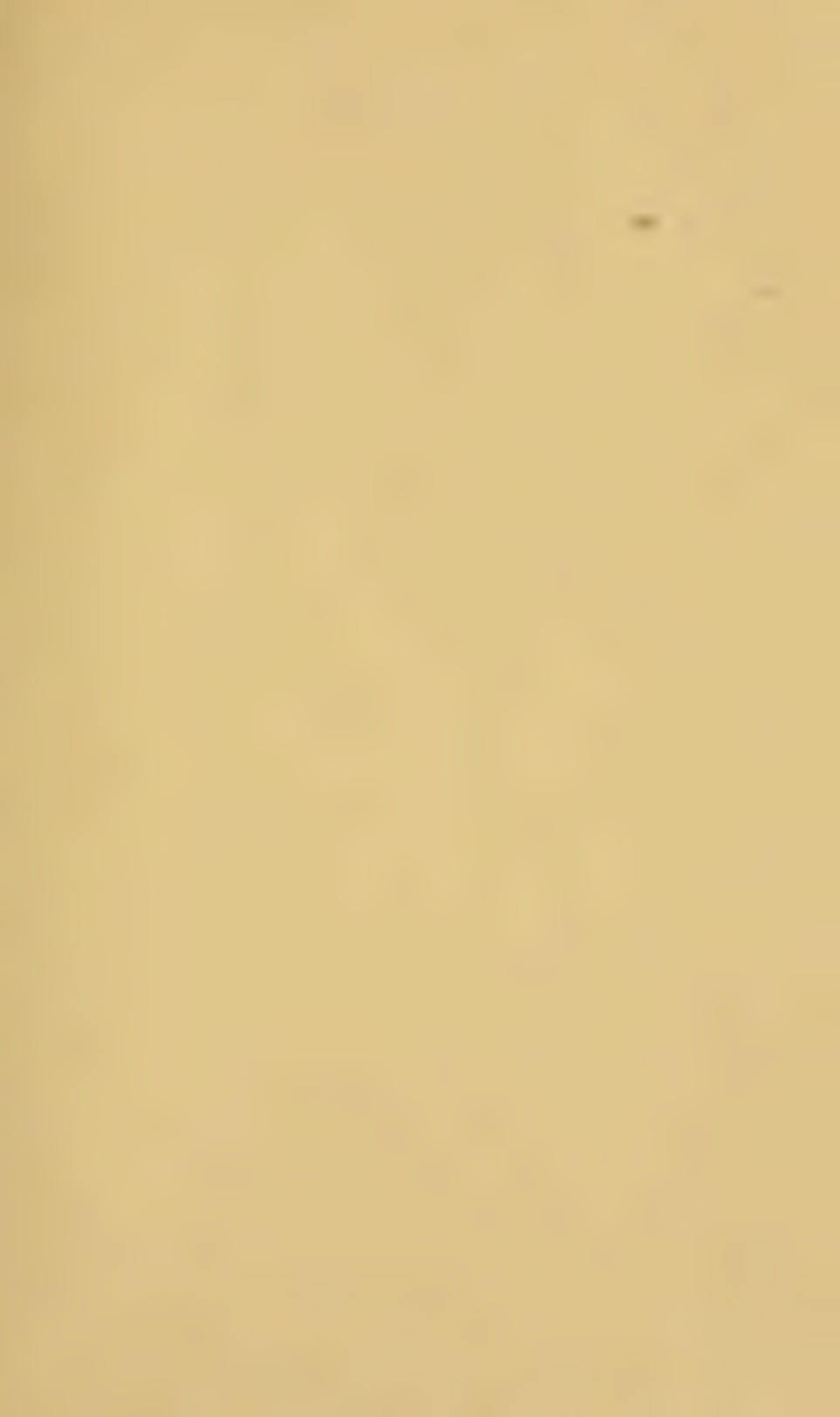
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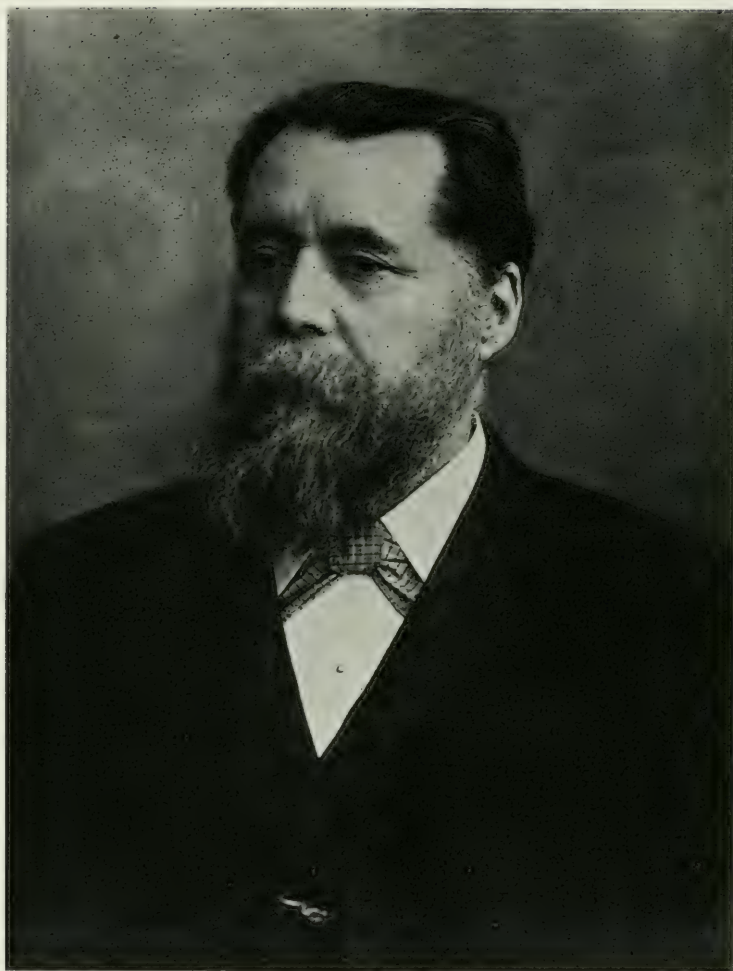
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**Out of print.

†Published version: *The Brain in Hominid Evolution*, New York: Columbia University Press, 1971.



James Anthony

JAMES ARTHUR

1842–1930

Born in Ireland and brought up in Glasgow, Scotland, James Arthur came to New York in 1871. Trained in mechanics and gear-cutting, he pursued a career in the manufacture and repair of machinery, during the course of which he founded a number of successful businesses and received patents on a variety of mechanical devices. His mechanical interests evolved early into a lifelong passion for horology, the science of measuring time, and he both made some remarkable clocks and assembled an important collection of old and rare timepieces.

Early in this century James Arthur became associated with the American Museum of Natural History, and began to expand his interest in time to evolutionary time, and his interest in mechanisms to that most precise and delicate mechanism of them all, the human brain. The ultimate expression of his fascination with evolution and the brain was James Arthur's bequest to the American Museum permitting the establishment of the James Arthur Lectures on the Evolution of the Human Brain. The first James Arthur Lecture was delivered on March 15, 1932, two years after Mr. Arthur's death, and the series has since continued annually, without interruption.

DO HORSES GALLOP IN THEIR SLEEP? CONSCIOUSNESS, EVOLUTION, AND THE PROBLEM OF ANIMAL MINDS

It is an honor to be asked to deliver the annual James Arthur Lecture on the Evolution of the Human Brain. The honor is especially great for me, because I'm not an expert on the evolution of the brain. I want to talk to you this evening not so much about brain evolution—which some of you know more about than I do—but rather about the evolution of the mind: in particular, that aspect of our mental lives that we call awareness or consciousness.

I've chosen to talk about consciousness for two reasons. For one thing, nobody understands much about it, and so I'm almost as qualified to talk to you about it as anybody is. More importantly, the appearance of consciousness is what gives the whole subject of brain evolution its importance. Why do I say this? Because consciousness is the only thing that gives importance to anything at all.

All values in the world have their source in the objective fact that the world contains subjective consciousness. That may sound like metaphysics, but it's really just a matter of common sense. To put it another way: life isn't worth anything if you spend it in a coma.

Let me propose a thought experiment. I would like you to imagine three things. First, imagine that we've discovered that a certain clump of nerve cells in the brain is essential for conscious awareness. Second, imagine that a certain drug suppresses neural activity in just this nucleus, with no effect on the rest of the brain. Subjects who take this drug do things as usual, but they experience nothing until the drug wears off. The drug converts them into sleepwalkers. Finally, imagine that I've developed a new form of this drug, which has *permanent* effects. It abolishes consciousness forever, with no effect on behavior. I want to test it on you. How much will you charge to take it?

I see no volunteers, and I think the question answers itself. Spending your life as a sleepwalker is equivalent to being dead; and so you will charge me whatever price you would charge to commit suicide. Some people might accept the deal, but only if their lives were so desperate that oblivion seemed attractive.

Oblivion attracts the wretched because the absence of consciousness erases all values, negative as well as positive. To the unconscious, nothing is either a blessing or a curse, any more than it is to an inanimate object. You are not being cruel to your car when you fail to service it, or kind when you rotate its tires. Nothing is either a benefit or an injury from a car's standpoint, because it has no standpoint. Having no awareness, it has no interests. And the same, I think, is true of other permanently unconscious things, both organic and inorganic. For example, a species has no interest in surviving, because it isn't the sort of thing that can have interests. When we speak of an extinct species as an evolutionary failure, we're being anthropomorphic. You can't fail without intentions; and intentions are impossible in the absence of consciousness. Even in the case of *human* life, our legal codes make similar judgments about hospital patients whose brains have gone electrically silent. These people are human, and alive; but because we believe them to be permanently unconscious, we deem them to have no further interests, and so we demote them to a purely instrumental value—for example, as a source for organ transplants.

These facts are fairly obvious, but I want to stress them here at the start of these remarks to dispel the notion that conscious awareness is too metaphysical and subjective a phenomenon for science to concern itself with. As the source of all value in our lives, it should be at the top of the scientific agenda. Yet in spite of its fundamental importance, consciousness is a subject that most scientists are reluctant to deal with. We know practically nothing about either its mechanisms or its evolution.

In fact, many distinguished scientists and philosophers believe that consciousness has no evolutionary history, because they think human beings are the only creatures that have it. Even many of those who suspect that some other animals may be conscious doubt that we can ever know for sure, and therefore would prefer to exclude this whole subject from the scientific world picture. Most scientists, I think, will admit in private that our close animal relatives probably have mental lives something like ours, because after all they have bodies and brains and behavior that resemble ours more or less closely. But a lot of scientists are reluctant to say so plainly

and publicly; and those that do can count on being accused of sentimentality and anthropomorphism.

I ran into this recently when I wrote a rejoinder to an opinion piece that appeared in a major biology journal. Its author had condemned animal-rights activists for failing to understand that an animal's major purpose in Nature is to be eaten by others. In replying, I asked what could possibly be meant by talking about an animal's purpose in Nature. Nature isn't the sort of thing that has purposes or intentions. Nature is just The Way Things Are. Only certain animals have purposes and intentions—and they never include being eaten by others. When the journal's editor read this, he at once demanded that I cite some published studies to support my dubious claim that *animals* can have intentions. So I smiled and changed the sentence to read, "Some animals (for example, human beings) have intentions." There were no more objections.

People have in fact done experimental studies to test the proposition that nonhuman animals sometimes have intentions (Heyes and Dickinson, 1993). But as far as I know, nobody has felt the need to run experiments to determine whether you and I have intentions. We all know that *we* ourselves have them; and we know that other people are built like us, and behave like us, and act as though they have intentions. That's all we need to know. Yet somehow the same sort of evidence doesn't settle the issue when other species are in question.

Animal intentionality, or what looks a lot like it, is of course a commonplace everyday phenomenon. For instance, most of us who own dogs have probably had the experience of seeing our dog search out a favorite toy and bring it to us in the hopes of getting us to play with him. It's difficult and awkward even to describe these familiar experiences without saying things like, "The dog was trying to find his ball," or "The dog wanted me to play with him." But scientists aren't supposed to say things like that, at least when we have our lab coats on. If we discuss such things at all, we prefer to do so in some way that doesn't involve attributing intentions or any other mental states to the dog.

There are at least two ways we can do this. First, we can use clumsy behavioral circumlocutions for mental language. Instead of

saying, “The dog looked for his ball until he found it,” we can say something like, “The dog exhibited repeated bouts of investigative behavior, which ceased after he contacted the ball.” This somehow manages to suggest that the dog wasn’t thinking about the ball while he was looking for it, and that he didn’t perceive anything when he got it in his mouth.

Second, if we find these circumlocutions silly and tedious, we can adopt some variant of what is sometimes called “logical behaviorism,” in which the mental words are still used but are redefined in terms of the probabilities of various behaviors. In this view, a dog’s intentions and desires and beliefs turn out, when properly understood, not to be something inside the dog, but theoretical constructs pinned on the dog by a human observer. Therefore, the human observer can know whether the dog has intentions and desires and beliefs, but the dog can’t. The philosopher Daniel Dennett is probably the best-known advocate of this position at the moment. In Dennett’s reading, dogs have real beliefs and intentions—but so do computers and thermostats and alarm clocks, because believing something is literally identical with *behaving* as though you believed it. The mental states that accompany your behavior are irrelevant; and in Dennett’s view, they’re unique to human beings anyway (Dennett, 1987a, 1987b, 1991, 1995).

Why do scientists and philosophers go through all these contortions to avoid attributing mental states to animals? There are several reasons. Some of them are better than others.

Let’s start with the best ones. There’s no doubt that sentimentality and uncritical anthropomorphism are real temptations, and that they should be avoided in describing and analyzing the behavior of non-human organisms. A lot of us succumb to these temptations. We all know people who insist on telling you what kind of music their begonia likes or what their cat thinks about Rush Limbaugh. These people are mistaken. And scientists sometimes make similar mistakes. Some of the early Darwinians in particular were guilty of this sort of thing. Because Darwin’s opponents often cited the mental and moral differences between people and beasts as reasons for rejecting the whole idea of evolution, many of his early followers tried to play down those differences by repeating anecdotes they had

heard about the nobility of dogs, the cunning of mules, and the self-sacrifice of chickens.

The British psychologist C. Lloyd Morgan was dismayed by the early Darwinians' uncritical attribution of human mental states to animals, and he tried to put a stop to it. In 1894, Morgan laid down the following law in his book, *An Introduction to Comparative Psychology*:

—In no case may we interpret an action as the outcome of the exercise of a higher psychological faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale.

Successive generations of experimental psychologists have adopted this dictum as a fundamental axiom called *Morgan's Canon*. It's generally thought of as a special case of Occam's Razor, the principle that you shouldn't make up entities unless you have to. For instance, you shouldn't posit a mysterious life force in living things if you can explain all the phenomena of life in terms of chemistry. Likewise, if you can explain an animal's behavior as, say, a conditioned reflex, you shouldn't try to interpret it as the outcome of volition or thinking. By this view, we are required to deny mental events in animals whenever we can, in the name of parsimony.

All of this sounds reasonable, but there's a fundamental flaw in it. Because *we* have mental events, we already know that there *are* such things in the universe. Denying them to animals therefore doesn't *save* anything; we have the same number of entities on our hands no matter what we decide about animal minds. Occam's Razor doesn't provide any support for Morgan's Canon. In fact, some animal-rights philosophers (e.g., Regan, 1983: 29) claim that Occam's Razor is on *their* side. They argue that if we're going to invoke intentions, desires, beliefs, and other mental phenomena in accounting for our own actions, we should explain other animals' behavior in similar terms whenever we can—again, in the name of parsimony.

Morgan himself agreed that it would be simpler to assume that other animals have mental lives like ours; but he insisted that simplicity is no guide to truth. He felt that his Canon was justified not by the principle of parsimony, but by the theory of evolution. His argument to that effect (Morgan, 1894: 55–59) involved a very 19th-

century picture of evolution as the grand story of our ancestors' climb from the primordial ooze up to the human condition, which furnishes the standard by which "psychical faculties" are to be judged as "higher" or "lower in the psychological scale." "Higher" here turns out to mean "distinctively human," and "lower" means "shared with other species." So the true, underlying meaning of Morgan's Canon is something like this:

—In no case may we interpret an animal's actions as the outcome of humanlike mental events, if we can find any other way of explaining them.

This still sounds like a prudent proposition. But why is it? Why should we assume a priori that if we have something, then animals don't? What risks, exactly, are we guarding against here? Why is it *safer* to assume that human properties are unique? Why wouldn't it be a safer bet to assume the opposite?

The problem with Morgan's Canon comes into sharp focus if we transfer the argument from the brain to the kidney. Consider this version:

In no case may we interpret an animal's urine as the outcome of humanlike biochemical processes, if we can find any other way of explaining it.

If Morgan's Canon represents a safe assumption, so does this one. But it's obvious that this version is ridiculous, and that physiologists would think I was crazy if I insisted that they adopt this rule to avoid the temptations of anthropomorphism. Then why does Morgan's Canon *seem* so much more plausible than this one? Are neurologists just more gullible than urologists? Or is there something special about events in the brain that makes them different from events in the kidneys?

Part of the answer, of course, is that we don't care about kidneys the way we care about brains, because brain events are a source of human status and kidney events are not. Our mental abilities are markers of the boundary between animals and people, which is one of the two primary lines that we use to divide up the moral universe. Because nonhuman animals lack some of our mental abilities, we regard them as property, to be used for our ends in any way we choose—on the dinner table, or in scientific experiments, or trans-

formed into soap and shoes and lampshades. The only moral constraint that we observe on our use of other animals is an obligation not to make them suffer. And we acknowledge *that* duty only because we believe that at least some of the animals are on our side of the *second* big line we draw across the moral landscape—the boundary between sentience and nonsentience, between things that are conscious and things that aren't. So both of our major moral boundaries are defined by things that go on in the brain.

Brain events, then, have moral implications that kidney events don't, which is why we're so generous about recognizing humanlike urine in other animals and so stingy about recognizing humanlike behavior. I want to point out in passing that the whole notion of "behavior" hinges on this moral aspect of neurology. When people like Stephen Gould argue that human behavior isn't biologically determined (e.g., Gould, 1981: 327), they aren't thinking about such body movements as the contractions of the heart or the intestines. Those movements are quite thoroughly determined biologically; but we don't think of them as *behavior*, because we don't regard ourselves as *responsible* for them. Having a spastic colon is not bad behavior. "Behavior" means *voluntary* movements—movements produced by striated muscle under conscious cortical control. If a movement is produced by cardiac or smooth muscle, or by striated muscle under the exclusive control of the brainstem or spinal cord, we don't call it behavior; we call it physiology. The distinction we draw between physiology and behavior is a projection of our concept of moral agency—which ultimately depends on the fact of consciousness. Unconscious actions are by definition involuntary.

Up to this point, I have been assuming that mental events are, or are produced by, events in the brain. Scientists rarely question this assumption. However, philosophers question it a lot. Some of them argue that mental events can't be equated with brain events, because we can see other people's brains but not their minds. Brain events, they point out, are objective and public; mental events are subjective and private. This is the other crucial difference between the brain and the kidneys—and the other source of scientists' uneasiness about the question of animal consciousness.

The intrinsic *subjectivity* of consciousness makes scientists un-

comfortable. Being conscious is the same thing as having private experiences; and the scientific method is fundamentally committed to the assumption that private experiences don't count as evidence. Only publicly accessible and repeatable experiences have that status. If somebody makes a claim that you can't check out for yourself, then you're not obliged to take it seriously. This makes science constitutionally anti-authoritarian, which is good; but it also makes it unreceptive to claims about consciousness and its contents. Most of the recent literature on the subject of consciousness is not really about consciousness at all, but about either neurology or behavior. These are public phenomena, and scientists know how to deal with them. So they spend a lot of time trying to convince themselves that studying these things is somehow the same thing as studying consciousness—like the drunken man in the story who lost his wallet in Central Park but went looking for it in Times Square because the light was better.

The field of computer science called artificial intelligence grew out of these assumptions. In a classic paper published in 1950, the English computer theorist Alan Turing offered a test for telling whether machines can think. He called it "the imitation game." Suppose, he said, that we can write a program that will exchange e-mail with you. If, after five minutes of sending messages back and forth, you can't tell whether you've been chatting with a human being or a computer, then the machine has a human mind—because that's what having a human mind means: being able to carry on a human conversation. What other test could there be? And Turing (1950) predicted that some of us would see such machines within our lifetimes. Here's the quote:

I believe that in about fifty years' time it will be possible to program computers, with a storage capacity of about 10^9 , to make them play the imitation game so well that an average interrogator will not have more than a 70 per cent chance of making the right identification after five minutes of questioning.

Check out those numbers. It's about fifty years later, and 10^9 equals around 16 megabytes. You can buy the supercomputer of Alan Turing's fondest dreams off the shelf at Sears for the price of a beat-up used car; and far bigger machines can be had at higher

prices. But none of them has yet been programmed to play the imitation game successfully. What went wrong?

I think what went wrong wasn't just Alan Turing but the whole Western conception of what it means to be human. Our traditions encourage us to define ourselves not by what we *are*, but by how we are *different*: to think of the human essence not in terms of our *properties*, but in terms of our *peculiarities*—the small subset of human traits that we don't share with any other creatures. Many of these human peculiarities hinge on our unique skill in manipulating symbols; and that also happens to be what philosophers get paid for doing. It's not surprising, therefore, that philosophers and professors from Plato on down to Noam Chomsky have told us that juggling words and numbers is the defining excellence that makes people special, and that animals that lack it are mere objects. Marcus Aurelius summed it up in this maxim (*Meditations*, 6.23): "Use animals and other things and objects freely; but behave in a social spirit toward human beings, because they can reason."

Many Western thinkers have gone further and insisted that because animals can't talk, their mental lives are defective in big ways, or even nonexistent. "Thinking," wrote Wittgenstein (1958: 6), "is essentially the activity of operating with signs." That view of thinking naturally appeals to college professors, who sometimes get so consumed by operating with signs that they wander around their campuses talking to themselves and tripping over shrubs. And because nonhuman animals aren't very good at operating with signs, many professorial types have been reluctant to grant that beasts can have mental lives at all. Others suspect that thinking also has something to do with not tripping over shrubs, and that dogs and cats and horses may be as good at it in most ways as a lot of college professors are—and infinitely better at it than any computer is.

Some people argue that since animals don't have words for things, they don't have *concepts*; they can't judge and classify sensations, and therefore they don't really perceive objects. All they do is respond to stimuli. A surprising number of Western philosophers and psychologists, from Augustine (*City of God*, 12.4) on down, have bought into this notion, but it seems to me to be demonstrably false. Many, and maybe most, of our concepts have no words attached to

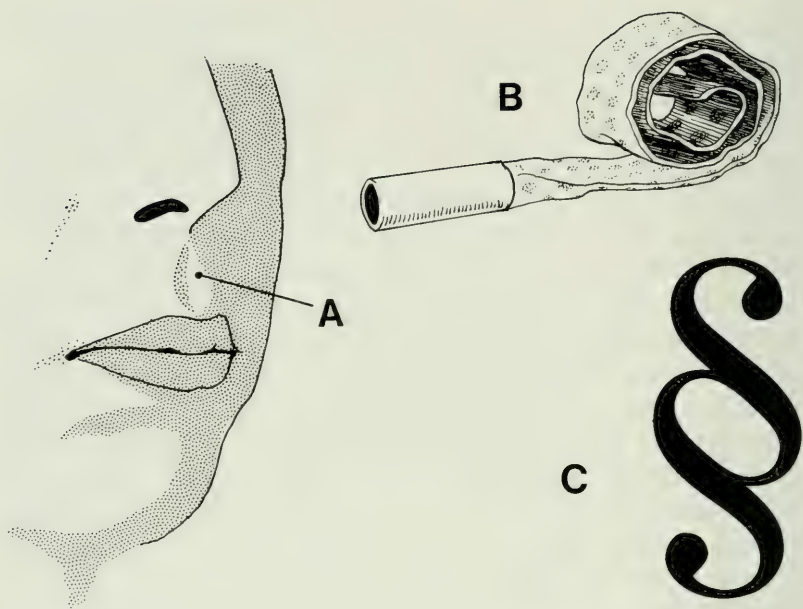


Fig. 1. Three examples of nonverbal concepts: (A) an anatomical feature, (B) an artifact, and (C) a written symbol.

them. Three examples—one natural object, one type of artifact, and one written symbol—are illustrated in figure 1. I suppose there are names for these things, but the only one *I* know is the first one; and I even had to look *that* one up—and I'm an anatomy professor. Yet we all recognize these things as representatives of familiar classes. And if *we* don't need words to have concepts, then neither do dogs, horses, and pigeons.

Because Western thinkers have always attached so much importance to juggling symbols as a marker of human status, and so little importance to walking around without tripping over things (which couldn't be very important, because a donkey can do it just as well as a philosopher), it was inevitable that when we managed to build a symbol-juggling engine—a machine that could beat us all at chess and prove the four-color theorem—our philosophers would try to persuade us that it was human. Once we taught it to play the imitation game, they assured us, it would be just like one of us. But so

far, it has proved impossible to program such an engine to succeed at the imitation game. The reason is that, although a computer has many of the symbol-manipulating abilities that we prize so highly, it lacks the subtler and more mysterious skills that come with being a sentient animal, inhabiting and experiencing the world in a living body.

Computer metaphors have come to dominate our thinking about brain processes and mental events. They predispose us to believe that mental events are *algorithmic*—that is, that they are produced by executing a programmatic list of logically connected instructions—and that digital computers (which are algorithm machines) will eventually become conscious if only we can run the right program on the right kind of hardware with the proper stored data. But as the philosopher John Searle (1992) has argued forcefully, there are good reasons for thinking that conscious awareness isn't, and can't be, produced by running a computer program.

A digital computer is essentially a grid of slots, each of which can be either full or empty. We think of these as ones and zeroes. Some of these slots are linked causally by rules of operation, which provide that when a certain pattern shows up in *this* area, the contents of other slots are changed in various ways, which may depend on the contents of yet *other* slots. In modern computers, the ones and zeroes are represented by electrical charges in semiconductors, but they could be represented by anything: holes punched in cards, or beads on wires, or eggs in egg cartons. The medium doesn't matter: what's important is the algorithm. All the operations that you do on a computer could be done in exactly the same way by giving a team of people written instructions for moving eggs around in a football field full of egg cartons, though of course it would take longer. (By the way, a football field full of egg cartons has about 1 megabyte of RAM.)

This fact poses problems for computational theories of the mind. If moving electrical charges around in a certain pattern can produce subjective awareness and bring a mind into existence, then so can moving around a collection of eggs in the same pattern; and if I knew how many eggs to use and what rules of operation to use in moving them, then I could make my egg collection think it was

Elizabeth Dole or the Wizard of Oz. I could get the same effects by making chalk marks on a blackboard, or waving semaphore flags, or singing songs, or tap dancing. All these processes can be computationally equivalent, with algorithms that correspond in every detail; but none of them seems like a plausible way of producing a subjective awareness. And since a digital computer is just another way of instantiating an algorithm, it seems impossible for such a device to become conscious. If we ever succeed in creating an artificial intelligence, it's going to have to be something more than an algorithm machine.

If consciousness isn't algorithmic, then how is it produced? We don't know. The machineries of consciousness are an almost perfect mystery. Neuroscientists and computer scientists have produced a lot of useful and suggestive models of how the brains of animals process sensory data and judge and discriminate among stimuli. We know that such mechanisms exist in our own brains, and that we need them to perceive the world. But although these perceptual mechanisms are *necessary* for consciousness, they aren't *sufficient*, because we can perceive things and respond to them without being aware of them. The unconscious mind is a real phenomenon. Freud's picture of it may have been wrong in its details, but he got the big picture right: most of our mental activity is carried out by subsidiary parts of the mind to which we don't have any direct conscious access.

One much-studied example of this is the phenomenon of blindsight. People with brain injuries to the visual cortex at the back of the head often go blind; they report seeing nothing, they can't read, they walk into things. But if you present things to their eyes and ask them just for fun to guess what they would be seeing if they *could* see, they guess with surprising accuracy. What seems to be happening is that visual centers in the older, subcortical parts of the brain are receiving and processing retinal input, and then forwarding it to the cortical speech centers along pathways that bypass the visual cortex—which are therefore not perceived *as vision* (Weiskrantz, 1986).

The reverse phenomenon, called perceptual defense, is more familiar. People confronted with unwelcome sights or sounds often

don't perceive them consciously, though you can show by monitoring their blood pressure or pupil dilation or other responses that they have in fact perceived them and interpreted them correctly. For example, if you present pairs of spoken words to people through stereo headphones and ask them whether they heard the same word in both ears, they fail to hear the difference between disparate pairs significantly more often if one of the two words is an obscenity. At least that used to be true when I ran that experiment in my undergraduate psych lab, though I imagine the perceptual threshold for tabooed words is lower now than it was back then.

Not only do we perceive many things unconsciously; we can act on those perceptions without being aware of our actions. The most spectacular example of this is sleepwalking.

Sleep takes several forms. In the living brain, waves of nerve-cell discharges travel across the surface of the cerebral cortex like the network of ripples on a swimming pool. We can detect, monitor, and record them as changes in electrical potential on the surface of the overlying scalp. Like the ripples on a pool, these brain waves vary in frequency and amplitude, from big and slow to fine and choppy. They're fine and choppy when we're awake; this is called the alpha rhythm. As we sink deeper and deeper into sleep, the waves become slower, bigger, and more synchronized, because the neurons in one area are all tending to fire at the same time. The waves become slowest and biggest in the so-called delta rhythms of deep sleep, in Stages III and IV. It's hard to wake people up from these stages. In normal awakening, the sleeping brain climbs back up this staircase, through all the successive stages of sleep, back to the alpha rhythms seen in both Stage I sleep and waking consciousness (Hobson, 1989).

Now, here's the strange part. Many people—as many as 30 percent of all children and 7 percent of adults—sometimes get up and start walking around during the deepest, most unconscious part of sleep, in Stage IV. Typically, sleepwalkers open their eyes, sit up in bed with a blank facial expression, pluck aimlessly at the bedclothes, and then rise up and walk. They ignore objects and people nearby, but they usually manage to get around without bumping into things. They may do very complicated and distinctively human things—

talk, make phone calls, get in a car and drive off, or even play musical instruments. Conversely, they may also do very dangerous and stupid things, like walking through glass doors or over cliffs. If you try to wake them up, they struggle violently to get away from you; and if you succeed in awakening them, they're totally confused and have no recollection of what they were doing or how they got there (Hartmann, 1983; Rauch and Stern, 1986; Reite et al., 1990; Thorpy, 1990).

The phenomenon of sleepwalking shows that you can get surprisingly complicated and even distinctively human behavior without consciousness. Some sleepwalkers could pass the Turing test 30% of the time (which is all that Turing demanded) with no difficulty. I know this because the one time I myself encountered a sleepwalker, it took me several minutes to recognize that she was unconscious; and I probably wouldn't have caught on at all if she hadn't been a family member whose behavior I knew very well. All this makes it much harder for us to find out anything about animal awareness. How do we know that animals aren't simply sleepwalking all the time, even when they appear to be awake? Do wolves hunt and horses gallop in their sleep, in the same way that a human somnambulist gets into a car and drives off on the freeway at 65 miles an hour? When the cock crows in the morning, is the farmer the only animal on the farm that wakes up? And if we can do so many things without being conscious, then why did consciousness evolve?

Let's start with that last question first. It's been proposed that consciousness permits you to construct objects in your mind out of the diverse input from several different senses (Jerison, 1973). When we see a car drive past, we don't separately hear its motor *and* see its body *and* smell its exhaust. We perceive one thing—a car passing by. We attribute the sight, sound, and smell to it as its properties; and we get out of the way to avoid the tactile sensations that we expect to go with them.

Neurobiologists refer to this as the “binding” phenomenon. Most animals pretty clearly don't have it. They don't exhibit what's called *cross-modal perception*; that is, they don't recognize an object through one sense if they've experienced it only through another.

They have separate and very mechanical responses to the inputs from different sense receptors. When a frog strikes at a fly, it doesn't see the fly as an object; it's just built to snap at any moving object overhead of a certain size (Barlow, 1953; Barlow et al., 1972). A frog will starve to death in the midst of a heap of freshly killed flies. It doesn't recognize them as flies, and it won't sniff or peck at them or try one to see if it tastes good, the way a mammal or a bird would. It seems reasonable to conclude that frogs aren't conscious. It also seems reasonable to think that frogs might be better off, other things being equal, if they *were* conscious and could perceive flies and other objects.

It has accordingly been suggested that binding and consciousness are different words for the same thing, and that consciousness is adaptive because it allows us to construct objects in our minds, benefit from cross-modal learning, and develop an internal map of the world that lets us anticipate what's going to happen and stay one jump ahead of things—instead of just producing knee-jerk responses to stimuli. If all this were true, then we could tell which animals were conscious by just testing them for cross-modal perception. And this does seem like a valid negative test; that is, animals like frogs, that *don't* have cross-modal perception, probably aren't conscious in any recognizable sense.

But the test won't work the other way around, as evidence *for* consciousness, because people can integrate different sensory modes while they're asleep. For example, sleepwalkers have been known to sit down and play the piano; and anybody who can do that must be putting hearing, touch, and proprioception together into a single experiential construct. If people can do this sort of thing in Stage IV sleep, then binding can take place without conscious awareness.

Then what does consciousness do for us? Well, why should we assume that it does anything? Some people have argued that it confers no adaptive advantage whatever—that it's just an incidental side effect of neurological complexity. But I think that idea can be rejected for Darwinian reasons. If consciousness were a useless epiphenomenon, natural selection would have operated to get rid of it somehow, since we have to pay a high price to have it.

The price we pay for consciousness is unconsciousness, of the

special and peculiar sort we call sleep. Mammalian sleep is a complicated and dangerous performance, and most animals don't do it. Invertebrates and cold-blooded vertebrates usually have daily periods of torpor when they hide and rest, but most of them show little or no correlated change in neural activity (Hartse, 1989). Among vertebrates, true sleep, involving a shift from fast to slow waves in the forebrain, appears to be limited to mammals and birds, though there are hints of it in a rudimentary form in some reptiles.

In birds and therian mammals (Hobson, 1989; Amlaner and Ball, 1989; Zepelin, 1994; Siegel et al., 1996), slow-wave sleep is interrupted at intervals by a second kind of sleep called REM (rapid eye movement) sleep. In REM sleep, the EEG goes back to the alpha rhythm. There are synchronized bursts of activity in different sensory areas of the cortex, as well as in the muscles of the eye, the middle ear, and the pinna. The eyes swing this way and that in coordinated tracking movements, in phase with the bursts of nerve-cell activity in the visual cortex; but they do so behind closed eyelids. In short, the brain appears to be seeing and hearing things that aren't there. In the human brain, at any rate, it's doing just that—because REM sleep is associated with dreaming. Another thing that happens during REM sleep is that the body's muscles lose their tone; we go totally limp from the neck down. This happens because nuclei in the brainstem spread chemicals around that raise the transmission threshold at the synapses linking the brain to the spinal cord. Sensory impulses coming in from the skin have a hard time getting through to the brain, and motor commands coming out of the brain don't get passed along to the spinal cord. In effect, the volume is turned down on the brain-body connections in both directions, so that the dreaming brain can attend to its own fantasies without responding to the world or jerking the body around. When these inhibitory mechanisms don't work in human beings, you get a pathological sort of sleepwalking called REM behavior disorder, in which sleepers act out their dreams—often with traumatic or even fatal results (Mahowald and Schenck, 1989).

Why do we sleep? On the face of it, it sounds like a bad idea to spend about a third of the day plunged into a limp, helpless trance state that leaves you unable to detect or react to danger. Mammalian

sleep is so dangerous, complicated, and time-consuming a performance that we feel sure it must have a payoff of some sort, but it's not really clear exactly what it is. Some argue that sleep serves to conserve energy, which is why we see it only in warm-blooded animals. The trouble with this theory is that mammalian sleep uses almost as much energy as wakeful resting. During 8 hours of sleep, a human being saves only about 120 calories (Zepelin, 1994)—the equivalent of a small glass of 2% milk, or three-quarters of a plain bagel. These savings don't seem worth spending a third of your life dead to the world. Another theory holds that sleep is a defense against predators; it's nature's way of telling us to hide when we don't need to be active (Webb, 1974). The problem with this story is that animals that don't sleep also find holes to hide in when they rest; and birds and mammals that are too big to hide in holes or climb trees still have to flop down and fall asleep every day, right out there on the prairie, exposed to every predator in the world. They do it as little as possible—a horse sleeps only about 3 hours a day, of which only some 35 minutes is spent lying down in REM-sleep atonia (Zepelin, 1994)—but they'd be better off if they didn't do it at all. They do it because they have to do it, not to save energy or avoid predators.

So sleep appears to be something imposed upon us, not by our environmental circumstances, but by the needs of the brain itself. Consciousness depletes or damages something in the waking brain, and we can't keep it up indefinitely. If we're forced to stay conscious around the clock, day after day, with no sleep, we soon start manifesting pathological symptoms, beginning with irritability and proceeding through fainting and hallucinations to metabolic collapse and death. And we seem to have a separate need for REM sleep in particular. If you keep waking people up whenever they enter the REM stage of the sleep cycle, they eventually start dropping straight into REM sleep without any slow-wave preliminaries. When this happens spontaneously, it results in a potentially serious behavioral disorder called narcolepsy.

So what is it that sleep does for the mammalian brain? Several people, including Francis Crick (Crick and Mitchison, 1983), have suggested that birds and mammals need to sleep because their be-

havior is flexible and based on learning and experience, instead of being just a collection of stimulus-response reflexes. This theory holds that behavioral flexibility—free will, if you like—introduces noise into the system and tends to mess up the innate, “hard-wired” responses and behaviors that these animals still need for survival. According to this model, sleep in general—and REM sleep in particular—acts every day to erase the neural irrelevancies, reset all the innate systems, and put everything back in working order, like rebooting a computer.

One fact that supports this model of sleep is the phenomenon called retrograde amnesia. When we’re awake, the things that drop out of short-term memory drop out more or less in the order they happened, so that it’s easier to remember things that happened two minutes ago than those that happened two hours ago. But when we drowse off, we start forgetting backwards, so that the last things learned are the first to be forgotten; and the longer we sleep, the further back in time the erasing of memory extends (Guilleminault and Dement, 1977). This shows that there is an active process of erasure that is peculiar to the process of sleep.

Another piece of evidence in favor of this model is that we get less and less sleep in general, and REM sleep in particular, as we age. In typical infant mammals, including human babies, over 80% of the sleep cycle is spent in REM sleep. As we reach adulthood, the world becomes more familiar and our behaviors more habitual; our brains get more canalized, new learning becomes less frequent and more difficult—and REM sleep drops to about 20% of the total cycle. Perhaps it does so because there is less new learning to be cleaned up after. It seems significant in this context that highly precocial infant mammals like guinea pigs and ungulates, which pop out of the uterus bright-eyed, bushy-tailed, and ready to start running, have low, adultlike percentages of REM sleep from day one on (Hobson, 1989; Zepelin, 1994).

As a sidelight, this model of sleep as an erasing and rebooting process suggests a possible explanation for the anomalous size of dolphin brains. Dolphins don’t appear to have REM sleep, and they exhibit slow-wave sleep on only one side of the brain at a time (Mukhametov, 1984). Being warm-blooded aquatic air-breathers,

they can't afford to have breathing reflexes; they'd drown if they started breathing automatically while unconscious. So when they sleep, they hang motionless or swim slowly along at the surface and one hemisphere stays awake to breathe and locomote, while the other drops into slow-wave sleep. The other peculiar fact about dolphin brains is that they're amazingly big for animals that act so stupid. Small dolphins have brain and body weights resembling our own (Cartmill, 1990); but their behavioral repertoire and general intelligence seem somewhat subhuman—comparable to, say, those of a chimpanzee. Perhaps dolphins need those big brains because each half sometimes has to function entirely on its own while the other half sleeps. This may also explain why each cerebral hemisphere in a dolphin has its own totally independent blood supply, and why the commissural connections between the two hemispheres are relatively tiny (Ridgway, 1986).

I want to bring things back to the beginning now, and return to the title of this talk, by reexamining the question of animal consciousness in the light of what we know about the structured unconsciousness of sleep. There are three basic operating states of the healthy human brain: (1) waking consciousness, with alpha rhythms, mental events, and awareness of the world; (2) slow-wave sleep, with no mental events or awareness; and (3) REM sleep, with no awareness of the world, but with alpha rhythms and hallucinatory mental events. In REM sleep, the brain is partly disconnected from the body to inhibit responses to those hallucinations.

Although sleep has some secondary ecological functions, which vary from species to species, the main needs it serves appear to be those of the brain. Evidently, sleep restores something that is damaged or depleted by being conscious, or by things that we do when we are conscious. Animals that are (probably) never conscious don't sleep; animals that we know are sometimes conscious—that is, people—are compelled to sleep. So are the other animals that we believe for various reasons may be conscious (i.e., mammals and birds). Moreover, their sleep resembles ours in detail. The sleep of birds is different from ours in some features, as you might expect in a trait evolved in parallel; but in most mammals, states (2) and (3) are the same as ours in every respect.

It seems accordingly reasonable to think that state (1) in these animals is also the same as ours, that it includes mental events and awareness of the world, and that the subjective differences for them between these three states parallel our own as closely as the objective differences do. If restorative theories of the function of sleep are correct—if sleep is in effect the price we pay for freedom of the will—then animals that sleep as we do must also sometimes wake up as we do and experience their presence in the world.

Because we can't directly observe the contents of animal minds, the evidence for animal consciousness is necessarily indirect. But it seems at least as persuasive as the indirect evidence that we have for other unobservable phenomena—for example, the Big Bang, or neutrinos, or human evolution. The philosophers and scientists who refuse to acknowledge that dogs feel pain when you kick them seem to me to suffer from the same kind of ingeniously willful ignorance that we see in a creationist who rejects the notion of evolution because he has never seen a fish turn into a chicken. I am inclined to believe that these philosophers and scientists are not so much concerned about understanding the universe as they are about looking tough-minded and spurning the temptations of anthropomorphism.

To most of us, the temptations of anthropomorphism don't look quite so dangerous as all that. Our close animal relatives, after all, *are* anthropomorphic in the literal sense of the word, which means "human-shaped." They have organs like ours, placed in the same relative positions. And interestingly enough, they seem to recognize the same correspondences we do. Despite the conspicuous differences in sight, feel, and smell between a human body and a dog's, a friendly dog will greet you by licking your face and sniffing your crotch, and a murderously angry dog will go for your throat—just as they would behave in similar moods toward members of their own species. These are sophisticated homology judgments; and they encompass not only anatomy, but behavior as well. Just as we anthropomorphize dogs, horses, and other animals, they cynomorphize and hippomorphize us—and each other—right back in the other direction.

Psychological accounts of these facts often treat them as mistakes—category errors resulting from what Hediger (1950, 1981)

has dubbed the "assimilation tendency" in social animals. I suggest that the assimilation tendency isn't a mistake, but an accurate perception of the way things are. In a world inhabited by closely related species, it confers an adaptive advantage. A gazelle that can tell when a lioness is thinking about hunting is less likely to be eaten; a lioness that can tell when a gazelle is thinking about bolting is less likely to go hungry. A man who doesn't notice that a horse is furiously angry, or a horse who can't make that sort of judgment about a human being, is correspondingly less likely to have offspring. Insofar as anthropomorphism recognizes and incorporates these facts about the world, it is not a vice but a survival skill. Indeed, one of the adaptive advantages of consciousness itself may lie precisely in the fact that it facilitates the reciprocal perception of other minds by analogy with our own—not just in our own species (Humphrey, 1987), but in others as well. If the construction of other minds in this way is both realistic and adaptively advantageous, as I believe that it is, then it is time to stop resisting its incorporation into the world view and vocabulary of science.

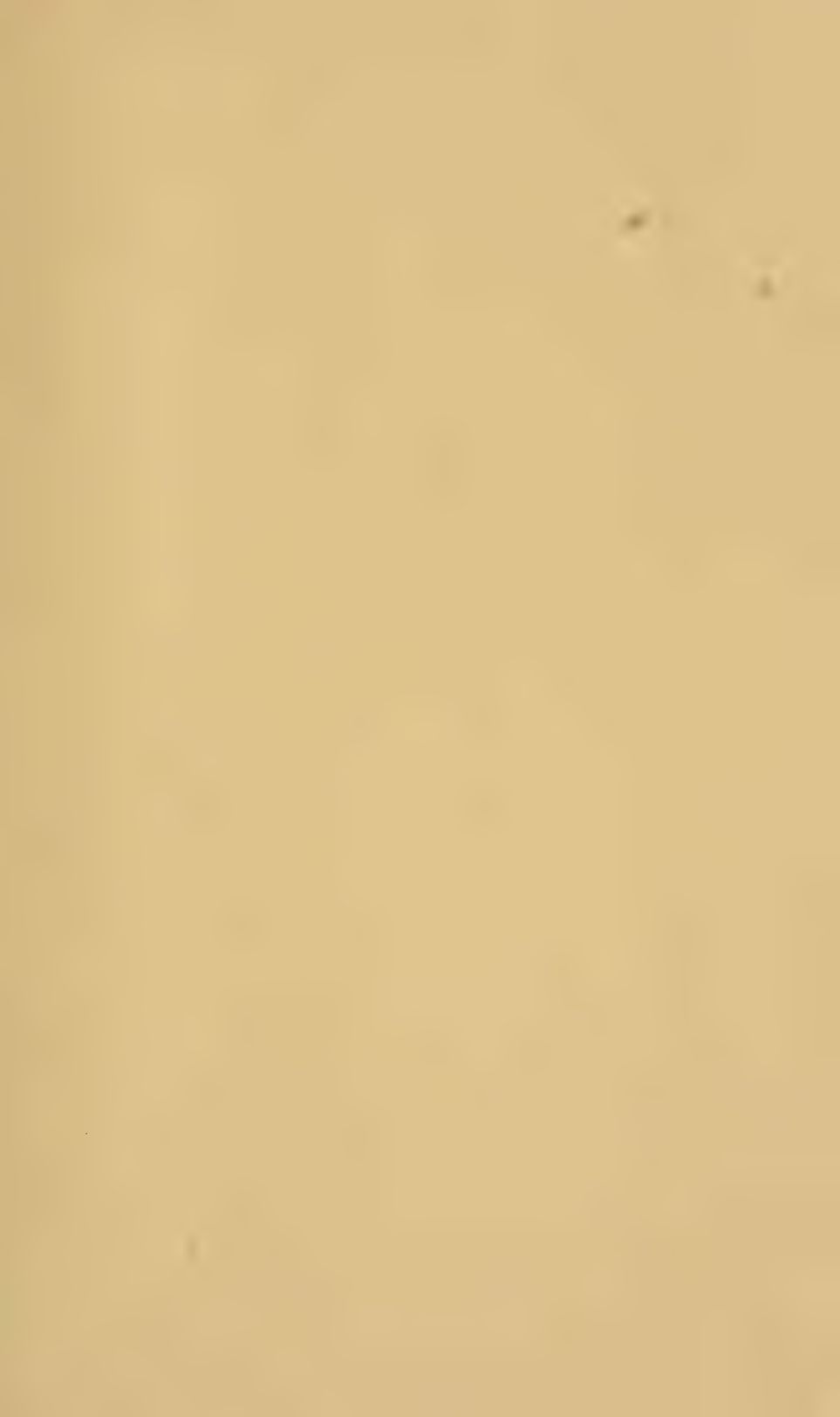
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